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OCT 27 1961
SCIENCE
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ECOLOGICAL MONOGRAPHS

VOL. 31

SUMMER 1961

NO. 3

OFFICIAL PUBLICATION OF THE ECOLOGICAL SOCIETY OF AMERICA

CONTENTS

The Role of Soil Arthropods in the Energetics of an Old Field Community

Manfred D. Engelmann
(Pp. 221-238)

The Fauna of Oyster Beds, with Special Reference to the Salinity Factor

Harry W. Wells
(Pp. 239-266)

Analysis of the Forest Floor Habitat with a Structural Classification of the Litter or L Layer

Harold Heatwole
(Pp. 267-283)

The Ecology of Blackbird (*Agelaius*) Social Systems

Gordon H. Orians
(Pp. 285-312)

PUBLISHED QUARTERLY BY DUKE UNIVERSITY PRESS
DURHAM, N. C., U. S. A.

ECOLOGICAL MONOGRAPHS

A QUARTERLY JOURNAL
FOR ALL PHASES OF BIOLOGY

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Subscription price: the United States, Canada, and the Pan-American Countries, \$6.00 per year; all other countries—\$6.00 a year additional for postage. Single numbers of the current volume are \$1.75. Back numbers, \$8.00 per volume, \$2.00 per number. Missing numbers will be supplied free when lost in the mails if written notice is received by the Circulation Manager within one month of date of issue. All remittances should be made payable to the Duke University Press, Box 6697, College Station, Durham, N. C.

Agents in Great Britain: The Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1. Prices can be had on application.

Second-class postage paid at Durham, N. C.

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THE ROLE OF SOIL ARTHROPODS IN THE ENERGETICS OF AN OLD FIELD COMMUNITY

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TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	221	Oxygen Consumption	225
MATERIALS AND METHODS	222	Annual Caloric Flow Through the Mite	
Sampling	222	Population	226
Extraction and Identification	222	Changes in Species Composition	228
Weighing and Respiration	223	Trophic Efficiencies	229
Feeding and Assimilation	224	DISCUSSION	232
PRESENTATION AND ANALYSIS OF DATA	224	SUMMARY	236
Biomass	224	LITERATURE CITED	237

INTRODUCTION

In a very stimulating paper (1942), the late R.L. Lindeman brought the problem of community energetics to the attention of the biologist, especially the ecologist. The study of this important problem did not spread, as one might have expected it to do, to all kinds of natural communities but remained focused upon the marine and fresh-water habitats. There are two reasons for the continued emphasis upon the aquatic habitats, the first and most important being the fact that the animal groups from these environments are comparatively well known taxonomically. Secondly, most of the support for studies in community energetics has come from various government and private agencies, who have recognized the implications of such work for fish production purposes. However, a critical evaluation of the general validity of Lindeman's concepts cannot be undertaken until data are obtained from a much wider spectrum of community types. This study is an attempt to apply the principles of community energetics to a terrestrial community with the intention of eventually broadening the scope of our knowledge in the area of community metabolism.

There are two aspects to any study of energetics: the field survey and the laboratory experiment. This division has led to two separate approaches to the problem which are ultimately dependent upon each other for the final answer. A field survey employs numerous methods to ascertain the density of each population present in the area. Such a study relies heavily upon the literature for information about the physiology and life history of various animals and plants in the community. An energy flow scheme is then constructed from the field data and the information in the literature. A few examples of this type of investigation are those of Lindeman (1942), and more recently Odum (1957) and Teal (1957). A laboratory study, on the other hand,

focuses attention upon the life history, physiology, and population dynamics of selected species under controlled conditions. The results of these investigations give information about the various efficiencies of which the species is capable. Examples of this type of study are those by Slobodkin (1959), Richman (1958), Trama (1957), and Armstrong (1960).

Several investigations have been concentrated upon the organisms living in various types of soil. Birch & Clark (1953) considered the status of the forest soil organisms as a study unit. Faunas of forest soils, especially in Europe, have been examined to a greater extent than those of prairie soils. Bornebusch (1930) pioneered with a study of several forest soils, ranging from pine woods to beech stands. He sampled the numbers and kinds of individuals in the soil, compared both species composition and numbers from the different stands, and attempted some studies of respiration and biomass on the soil animals. The sampling methods used by Bornebusch were inadequate, and his density estimates are low (Birch & Clark, 1953). Van der Drift (1950) has made one of the more recent studies on the forest arthropods, and this work contains an extensive bibliography. The work is mainly concerned with numbers of individuals and taxa, with the addition of some biomass estimates. Wallwork (1959) deals with several aspects of the population dynamics of some forest soil mites found in the United States. Extensions of the forest floor (such as tree holes) and specialized habitats have been considered by Park and his students (Park *et al.* 1950, Park & Auerbach 1954, Winston 1956).

Soil communities of fields and pastures have been studied by Salt *et al.* (1948), MacFadyen (1952), and Hairston & Byers (1954). Their papers are mainly concerned with numbers of individuals and distribution of animals in the community, although MacFadyen gives biomass data where possible. The Europeans have done more work on the soil arthro-

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Pods because the taxonomy of their soil groups is relatively well known. The taxonomic work on these same groups in America has been neglected, with many groups unworked for 40 years or more.

The soil arthropods of an abandoned field were chosen for the study discussed in this paper. Both laboratory and field studies were undertaken. The field chosen for study is located on the University of Michigan's Edwin S. George Reserve, 4.5 mi west of Pinckney, Livingston Co., Mich. Evans & Cain (1952) and Evans & Dahl (1955) have described the vegetation of this field; Talbot (1953, 1954) has investigated the ant populations; Hairston & Byers (1954) have sampled the soil arthropods; and Evans & Lanham (1960) have examined the insect fauna of the herbaceous stratum. According to Evans & Dahl, the climate is a humid, mesothermal one, with mean monthly temperatures ranging from -4°C in January to 23°C in July, with a mean annual precipitation of 78 cm well distributed throughout the year. The soil is a sandy loam with very good drainage. The humus layer of the soil ranges from 2.5 to 3.6 cm in depth. Vegetation of the field consists of grasses (*Poa*, *Aristida*, *Setaria*, and *Lepidoloma*), forbs (*Antennaria*, *Lespedeza*, *Rumex*, and *Solidago*), mosses (*Ceratodon* and *Polytrichum*), and lichens (*Cladonia*). The field has 2 distinct vegetation types or associations. Several depressions or swales are found in various areas of the field. These depressions have a dense cover of Kentucky blue grass, *Poa pratensis*, interspersed with the common milkweed, *Asclepias syriaca*. The rest of the field is higher and generally dominated by Canadian blue grass, *Poa compressa*, although there are patches of other grasses which displace the Canadian blue grass. Hairston (1959) found a difference in the soil fauna between the upland and the swales; therefore, these 2 areas are considered to be separate communities. In the present study only the upland community was considered.

The major goals of this study were (1) to determine the position of the oribatid mites in the food web, and (2) to indicate their role in the soil industry. Secondary goals included (3) determination of the ecological efficiency value for the soil herbivores, (4) comparison of this value with those obtained from aquatic studies, and (5) evaluation of the hypothesis that all communities operate on the same energetic principles.

I wish to acknowledge the following persons for their assistance during the course of my work: I. J. Cantrall, for permission to work on the Edwin S. George Reserve; F. E. Smith and P. Ovenberg, for their help with the regression calculations; L. B. Slobodkin, for advice on ecological efficiencies; and G. H. Lauff, for his sponsorship of the radioactive-labeling work. Special thanks are due my wife, Patricia, who typed the manuscript and helped with the editing; the members of my doctoral committee, W. R. Dawson, F. C. Evans, and A. H. Smith, who gave assistance during the course of the investigation and in the writing of the manuscript; and my chair-

man, N. G. Hairston, who gave encouragement and valuable help through the entire period of this endeavor.

MATERIALS AND METHODS

In evaluating the role of the arthropods in the soil of the old field, the following information was considered necessary to make up an energy balance sheet: the number of individuals present during the year; their reproductive rates and generation times; their body weights, and the amount of energy represented by these weights; and their metabolic energy. Despite the number of soil sampling studies, information about the soil arthropods is scanty. Data necessary to draw up the energy balance sheet were obtained by the following sampling and experimental techniques.

SAMPLING

A sampling program was employed to obtain estimates of the numbers of individuals present in the soil during the year. Hairston & Byers (1954) carried out an extensive program on the old field during the years 1949 and 1950; therefore, only a limited sampling program was undertaken in 1958. Sampling tubes 6.3 cm in diameter and 12.5 cm long were employed once each month to remove 3 plugs of soil from the central part of the old field. The sampling sites were chosen at random before the time of collection. The soil plugs were kept in the sample tubes and transported to the laboratory in plastic bags. This technique minimized moisture loss and kept the soil plug intact.

EXTRACTION AND IDENTIFICATION

Tullgren extraction (Park & Auerbach 1954) was used to remove the arthropods from the soil plugs. The soil plug in its sample tube was placed upside down in the Tullgren funnel. A 40-watt bulb furnished the heat and light source. The arthropods were caught in a jar containing 70% alcohol. The animals were then counted under a dissecting microscope.

The oribatid mites were the most intensively studied group of the soil arthropods found in the old-field samples. These small mites are found in forest and prairie soils all over the world; those found on the old field ranged from .1 to .9 mm. in length. Some of these mites are soft-bodied in all stages; however, most of the individuals from the samples studied were of species in which the adult has a thick chitinous exoskeleton and differs in appearance from the immature stages.

Taxonomically this group has received little attention. Although in Europe the taxonomic relationships of these mites are relatively well-known because of the work of men like Grandjean, work to date on forms from the Western Hemisphere has been of a pioneer nature. In recent years Dr. Tyler Woolley has begun a detailed study of the systematics of the Oribatidae, but the task is a very complicated one, and it will be a long time before the picture is in any way complete. Hence, for the

purpose of the research reported in this paper, a numbering device was substituted for species designations. The system was modeled after the one used by Hairston & Byers in their work on the field populations and proved a convenient tool for preliminary identification of different groups. Each recognized kind of mite was given a number and specimens were sent to specialists for future study. The immature forms which differ from the adults in appearance were probably placed in a different category. The immature forms, however, are rather infrequent in the samples. Therefore this source of error is probably not a major concern.

Live arthropods were caught in jars containing water (Engelmann 1956). The animals were cultured in jars which had a flooring of plaster of paris and charcoal (Rohde 1956). The jars were supplied with various types of food, and the plaster was kept moist. The most successful diet for the arthropods in culture consisted of washed, pulverized organic material found on the surface of the soil, supplemented with dried yeast (*Saccharomyces*) which had been suspended in water. The yeast was dropped onto the bottom of the "nest" in very small quantities. Funga (*Mycena*, *Aspergillus*, *Agaricus*, and others) were also used as a source of food at various times.

WEIGHT AND RESPIRATION

A quartz-helix balance sensitive to 2.5 μ g was used to weigh the arthropods. Many of the animals weighed less than a microgram, so that a number of individuals had to be weighed at one time in order to register on the scale; the weights are therefore averages in most cases. The animals were killed by immersion in alcohol for a few minutes. They were then transferred to weighing pans and placed in a desiccator for 24 hours or more. When removed from the desiccator, the dried animals began to take up water from the air at a rapid rate, until an equilibrium was reached in about 5 minutes. Consequently some moisture was probably taken up by the animals during this weighing procedure, which required approximately 1.5 minutes per measurement.

Respiration data for the soil arthropods were obtained with the Warburg respirometer (Umbreit 1949) and a modification of the insect respirometer of Smith & Douglas (1949). This latter apparatus proved to be most convenient and was used most frequently. The Smith-Douglas respirometer was modified by substituting small glass vials with ground glass necks for the large brass chamber of the original model. The bottom half of the vial was lined with moist filter paper and closed with a piece of sterile cotton after the arthropods had been placed

TABLE 1. Numbers of individuals of the oribatid mite species found in 22 soil samples from an old field, Edwin S. George Reserve, Livingston Co., Mich.

? indicates sample destroyed before species was counted.

Oribatid mite species no.	DATES OF SAMPLES																						Totals
	Dec. 1, '57	Dec. 1, '57	Jan. 3, '58	Feb. 8, '58	Mar. 3, '58	Apr. 13, '58	Apr. 13, '58	May 4, '58	June 6, '58	July 7, '58	Aug. 8, '58	Aug. 8, '58	Sept. 2, '58	Sept. 2, '58	Oct. 4, '58	Oct. 4, '58	Oct. 31, '58	Oct. 31, '58	Dec. 12, '58	Dec. 12, '58	Jan. 9, '59	Jan. 9, '59	
101	31	12	12	19	25	37	14	4	27	19	28	79	0	13	5	0	5	7	5	20	26	12	400
102	0	0	2	10	1	50	1	2	1	0	0	0	0	0	4	0	12	3	16	2	1	4	109
103	7	2	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	15
105	171	16	15	17	99	14	35	40	10	5	47	181	6	6	6	13	247	0	35	66	138	15	1182
108a	4	4	2	2	2	7	3	1	9	0	0	17	1	0	2	8	6	1	6	4	13	5	97
108c	3	6	0	11	0	25	5	0	0	0	0	1	0	1	1	1	19	6	12	2	1	0	94
108d	2	0	1	3	3	7	9	8	0	0	3	2	1	7	6	2	5	0	13	0	5	0	77
108e	0	0	0	0	0	4	?	1	0	0	1	0	0	0	0	0	6	0	0	1	0	0	13
109	0	0	1	2	0	2	0	0	0	0	0	0	0	0	0	0	0	1	23	0	1	0	30
110	0	13	2	0	0	0	2	0	2	0	0	0	0	4	1	1	0	2	0	0	5	1	33
111	0	0	0	0	0	0	0	0	0	0	0	10	0	0	1	0	1	0	0	0	0	0	12
112a	0	0	0	9	6	17	0	0	7	0	0	0	0	1	6	0	7	0	17	0	1	6	77
112b	0	0	0	0	0	0	0	2	7	2	0	3	0	3	3	0	0	0	0	0	0	0	20
113	0	0	0	0	11	0	0	1	0	0	0	1	0	0	0	2	0	1	0	0	0	0	16
114	4	4	17	7	1	1	2	0	0	0	1	8	0	1	0	15	0	0	1	0	0	6	68
115	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
116	0	0	0	0	0	0	0	0	2	0	0	4	0	1	2	0	3	0	1	0	0	0	13
117	3	0	4	8	0	0	0	1	2	0	0	0	0	0	4	2	1	1	25	14	6	3	74
118	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
119	0	0	0	1	0	2	0	3	0	0	0	0	0	0	0	0	1	0	2	2	0	0	11
120	0	0	0	25	8	66	?	11	7	31	37	54	27	31	35	5	47	3	26	37	4	2	456
121	10	5	0	0	0	0	0	4	2	0	0	0	0	0	2	1	4	2	1	0	0	0	31
126	?	?	7	89	6	42	?	1	4	3	2	5	10	30	8	3	48	9	60	0	61	20	408
128	?	?	0	0	4	0	?	32	7	4	15	8	0	8	155	11	46	0	139	153	0	2	584
Total...	235	62	68	203	166	275	71	111	87	64	134	373	45	107	241	64	458	36	383	301	262	76	3822

on the filter paper. A roll of filter paper soaked in .1 molar NaOH was placed in the upper end of the vial. The manometer consisted of a length of thick-walled capillary tubing with a bore of .5 mm. Colored water containing a detergent was used as manometer fluid. The respirometers were immersed in a water bath which maintained a temperature of 24°-25° C during the course of the experiment.

FEEDING AND ASSIMILATION

A radioactive labeling technique was used to make estimates of food ingestion and assimilation (Trama 1957). Yeast was labeled with radioactive glycine C¹⁴. A known quantity of the yeast was plated on a counting planchet and radioactivity determined in a gas flow geiger counter. This procedure yielded an estimate of the number of disintegrations per unit of time per unit of weight of yeast. The yeast was then presented to the animals for a period of time, the animals were killed and dissolved in hot formamide and plated on a planchet. The disintegrations per unit of time obtained from the dissolved animals were then translated into grams of yeast contained in the body of the animal at the time of death. When the animals were allowed to post-absorb before being killed, an assimilation rate was estimated.

A bomb calorimeter was used to obtain estimates of the caloric contents of various substances including vascular plant material, fungi, and insect larvae (Richman 1958).

PRESENTATION AND ANALYSIS OF DATA

The numbers of oribatid mites in the various species categories found in 22 samples taken over a 13-month period are given in Table 1. Species categories 101, 105, and 120 are found in most of the samples and are probably the more characteristic species of the field's upland. Species 115 and 118 were found only once and are most likely to be "accidentals". Yearly population patterns fell into 3 main types: populations with a relatively constant level through the year, populations largely restricted to the summer months, and populations showing increased numbers in both spring and fall. Species 101, 105, and 120 show no marked population peak, species 112b and 116 were taken only in summer, and the rest of the species show a spring population peak and a fall population peak. The fall population peak is usually greater than the one in the spring. This double peak has been observed in other oribatid populations (Sengbusch 1954) and has implications for the turnover rate of the populations concerned. Sengbusch believes that this double peak can be explained by the presence of two reproductive periods each year, one in the spring and one in the fall. Hairston & Byers (1954) give good evidence for the vertical migration of soil arthropods; therefore, the spring peak could also be explained by the return of the adults to the surface layers of the soil.

The total numbers of each species of mite in the 22 samples were divided by the number of sam-

TABLE 2. Numbers, weights, and biomasses of the oribatid mites found in an average soil sample (area 31.2 cm²) from an abandoned field in southeastern Michigan, 1958.

Species Category	Mean No. of Individuals Per Sample	Mean Wt. of Individual (μ g)	Species Biomass (mg/m ²)
101.....	18.20	1.50	8.750
102.....	5.00	2.00	3.205
103.....	0.68	15.60	3.397
105.....	53.70	0.70	12.019
108a.....	4.40	1.00	1.410
108c.....	4.30	0.51	0.705
108d.....	3.50	0.43	0.481
108e.....	0.60	0.33*	0.064
109.....	1.40	2.43	1.090
110.....	1.50	5.00	2.404
111.....	0.50	12.00*	1.923
112a.....	3.50	0.74*	0.833
112b.....	0.90	0.89*	0.250
113.....	0.70	0.71*	0.151
114.....	3.10	5.49	5.449
115.....	0.05	4.00*	0.074
116.....	0.60	0.33*	0.077
117.....	3.40	1.00	1.090
118.....	0.05	2.00*	0.029
119.....	0.50	0.20*	0.035
120.....	21.70	3.50*	2.436
121.....	1.40	7.15	3.205
126.....	21.50	0.31*	2.147
128.....	30.70	0.27	2.660
Totals.....	181.88	—	53.884

* Weight derived from regression equation.

ples to secure "average sample" figures for the thirteen months (Table 2). Weights were also obtained for each mite species. These figures were used to calculate the biomass of the oribatids found in an average sample (Table 2).

BIOMASS

Fig. 1 shows, on a double log plot, the relationship of the length-width index, i.e., the length times the width of the animal measured in microns, to the weight of the animal, in micrograms. The line was fitted to the points by means of the standard regression technique (the least squares method). The correlation coefficient of the points to the line is .85, and a *t* value of 12.0 is significant at a probability of less than .01. The animals were measured after they had been mounted on slides in balsam. This point is important, for there is some compression of the animal on the slide which increases the lateral dimensions, thus increasing the frontal area about 20%. The weight of slide-mounted animals was estimated from the following formula: Log weight of animal in micrograms = 1.32 [log length \times log width (in microns)] - 5.87. Neither length nor volume measurements showed a linear relationship when plotted against weight. The explanation for this is that the exoskeleton and muscles attached to it comprise most of the weight of these arthropods. Dry weight, therefore, becomes some function of the surface area rather than of volume. The length-

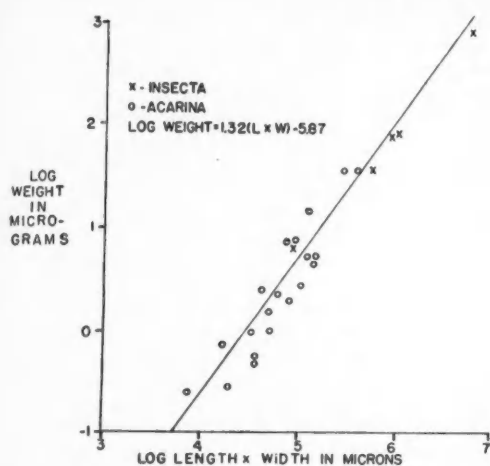


FIG. 1. The relationship of weight to length-width index in twenty five terrestrial arthropods. Data from Acarina (o) and Insecta (x) were used to make the plot.

width index is apparently some constant proportion of the total surface area (about 40%) and can therefore be used as a satisfactory measure.

The biomass for each species category was calculated from the weights obtained by direct weighing or from the regression equation (Table 2). A total of about 54 milligrams of oribatid mites was estimated for each square meter of upland of the old field. This estimate of standing crop was then converted into energy units by the assumption that a gram of arthropod protoplasm is equivalent to 5000 gram calories of energy. Culture methods did not allow the accumulation of enough material to make an actual assay of oribatid protoplasm; however, some calorimetry was done on fourth instar larvae of *Tenebrio molitor*. Larvae taken directly from culture and homogenized had a caloric content of 6578.9 cal/gm; fat-extracted individuals had a caloric content of 4858.1 cal/gm, and the exoskeletons (formamide-treated larvae) contained 4978.0 cal/gm. In a table compiled by Golley (1959), caloric values for the animal material tested ranged from 1900 cal/gm to 6200 cal/gm, with most of the values falling between 4000 and 5500 cal/gm. The assumption of 5000 cal/gm is, therefore, not an unreasonable approximation at the present time. The product of the total estimated standing crop (54 mg) times the mean caloric content (5000 cal/gm) gives an estimate of 270 cal of oribatid mites found to a depth of 12.5 cm on each square meter of upland.

When a population is in a "steady state" condition the total production biomass will remain the same from year to year, although during the year the standing crop biomass may fluctuate around some mean value. However, the standing crop gives little indication *per se* of the energy flow through the population. Energy flows into the population

in the form of food and flows out of the population in the form of respiration and dead individuals. As far as the population is concerned, egested or defecated food has never entered the protoplasm of the population. In this sense, then, the digestive tract of the animal can be considered an extension of the external environment. Therefore, only the functions of respiration rate, feeding rate, and death rate need be estimated to describe the basic energy characteristics of the population.

OXYGEN CONSUMPTION

Data on oxygen consumption by various arthropods were obtained with the aid of respirometers (Table 3). Technical difficulties prevented acquisition of respiration information from all of the soil arthropods; therefore, some other approach was needed to obtain estimates of the respiration of these animals. Data of Bornebusch (1931) were used with the data from Table 3 to plot the log of the total respiration of the individual against the log of the total body weight (Fig. 2). The slopes for the 2 sets of points are .74 and .85. The common regression line for all the points has a slope of .84. There is no significant difference between the 3

TABLE 3. Respiration of soil arthropods at 25°C in the laboratory.

Species	Weight μg	μl/ ind./hr. (Mean)	Range	s	Coeff. of variation	Avg. μl/ mg. per hour
Oribatidae <i>Oppia nova</i>	1.0	.0065	.0227- .0013	.0066	1.01	6.5
Oribatidae species 101.	1.5	.0024	—	—	—	1.6
Oribatidae Species 102.	2.0	.0044	.0041- .0050	.0052	.118	2.2
Acaridae <i>Tyroglyphus finteri</i>	2.3	.017	.0035- .0110	.01085	.61	7.4
Oribatidae Species 15.	11.05	.0215	—	—	—	1.95
Scydmaenidae Species 7 Larva.	13.6	.08	—	—	—	5.9
Oribatidae <i>Cassida</i> (mixed instars).	15.56	.0138	—	—	—	0.89
Oribatidae Species 12.	26.52	.0107	—	—	—	0.4
Mesostigmata Species 14.	40.1	.0305	—	—	—	0.76
Scydmaenidae Species 1 larva.	45.25	.140	—	—	—	3.1
Psolaphidae <i>Reichenbachia</i>	76.6	.145	—	—	—	1.9
Staphylinidae Species 4.	86.25	.215	—	—	—	2.5
Staphylinidae Species 3.	88.75	.061	—	—	—	0.7
Staphylinidae Species 6.	96.5	.18	—	—	—	1.9
Formicidae <i>Ponaria</i> (worker)	187.3	.24	—	—	—	1.3
Isopoda <i>Armadillidium vulgare</i> (Juvenal).	636.2	1.118	—	—	—	1.8
Carabidae Species 2.	891.0	.238	—	—	—	0.27
Scarabaeidae <i>Geotrupes</i>	160300.0	120.5	—	—	—	0.75

lines. A slope of .85-.90 is common for a great number of invertebrates (Zeuthen 1953). The *t* test values for each of the regressions are highly significant (*P* less than .01). The following formula was used to estimate the respiration of an animal when the weight was known:

Log respiration ($\mu\text{l } 10^{-3}$) = .85 (log weight in micrograms) + .44.

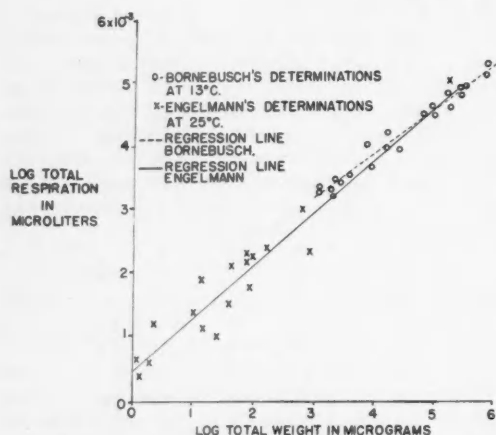


FIG. 2. Respiration-weight relationship in forty terrestrial arthropods. Data from the study of Bornebusch (1930) and from the present study were used to make the plot.

If the rates of oxygen consumption obtained from the respiration studies or from the regression equation are multiplied by the number of individuals in each species category, we obtain estimates of the

TABLE 4. Oxygen consumed and calories burned by the oribatid mites found in an average sample of 12.5 cm depth extrapolated to an area of 1 m², from an abandoned field in southeastern Michigan, 1958.

Species category	Oxygen consumption** for total population μl O ₂ /day	ENERGY EXPENDITURE OF TOTAL POPULATION	
		gm cal per 24 hours†	gm cal per year
101.....	336.205*	1.62173	192.98
102.....	169.224*	0.81728	97.25
103.....	302.873	1.46148	173.91
105.....	838.428	4.04471	481.30
108a.....	145.507*	0.70190	83.52
108e.....	50.639	0.24358	28.98
108d.....	26.602	0.12820	15.26
108e.....	4.808	0.02244	2.67
109.....	127.559	0.61536	73.22
110.....	124.675	0.60254	71.70
111.....	84.933	0.41024	48.82
112a.....	58.331	0.28204	33.56
112b.....	16.987	0.08333	9.92
113.....	8.654	0.04167	4.96
114.....	279.156	1.34610	160.18
115.....	3.846	0.01923	2.29
116.....	5.769	0.02885	3.43
117.....	72.113	0.34935	41.57
118.....	1.603	0.00641	0.76
119.....	2.885	0.01282	1.53
120.....	216.658	1.04483	124.32
121.....	126.277	0.60895	72.46
126.....	205.120	0.98714	117.46
128.....	214.735	1.03522	123.19
Totals:.....	3423.587	16.51538	1965.24

* From actual respiration measurement.

** Recorded at 25°C.

† Assuming an average value of .0048 calories per microliter.

amount of oxygen used by the population each hour, and these can be extrapolated to the daily oxygen consumption (Table 4). The total oribatid oxygen consumption per day was estimated at 3424 microliters. The caloric values of the oxygen consumed can be obtained if the RQ is known (Brody 1945: 310). Although no RQ is known for oribatid mites, the RQ of a resting insect is .82 (Roeder 1953), and the caloric equivalent of a microliter of oxygen at this RQ is .0048 cal. If this factor is applied to the data, an estimated 16.5 cal per day are burned by the total oribatid fauna (Table 4). Since these animals are poikilotherms, they will not function at the same rate throughout the year. The respiration-temperature curve of Krogh (1941: 6) and the monthly mean air temperatures of Ann Arbor (Clim. data, 1958) were used to determine the rates of respiration of the mites for each month. This was equivalent to 4 months of metabolic rate of 25° C. These calculations yield an estimate of 1965 calories respired by the oribatids over the period of a year (Table 4). An estimate of respiration based upon Krogh's curve may be too low, because many invertebrates are capable of some metabolic adjustment (Uvarov 1931, Agrell 1947, Bullock 1955, Fry 1958). Such adjustment could be advantageous to a soil dwelling organism, since the moist part of the year is usually the cold part of the year (spring, fall and winter). The soil arthropods require moist surroundings both because they are subject to desiccation, and because their food source requires moisture.

ANNUAL CALORIC FLOW THROUGH THE MITE POPULATION

Information on the feeding rates of the oribatid mites came from two sources: direct weight experiments and radioactive tracer studies. The 2 methods yielded different results. The radio-tracer work gave an estimate of 40% body weight ingested at the end of a 24-hour feeding period, while the direct weighing technique gave estimates of from 90-110% body weight ingested after the same time interval. This discrepancy was explained when it became evident that the mites were contaminating their food source by fungi carried into the culture in their digestive tracts or on their bodies. The growing fungi as well as the mites consumed the food, and, therefore, the loss of weight in the food planchet was more than doubled. The use of food by both mites and fungi produced the apparent high ingestion rate of the weight experiments. Radio-tracer work gave an estimate of 8% body weight assimilated at the end of 24 hrs. The direct weighing technique gave an estimate of 13% body weight egested per day. Since the contamination factor would also affect the latter estimate, this should be multiplied by a factor of 2.3 (the rate of consumption of mite feces by fungi in the cultures). Thus the more probable value is approximately 30% of the body weight egested by the mites each day.

Using a respiration factor of 4 months of full activity as a year's activity and a value of 4000

calories per gram of food material, it was estimated that 10,248 calories are ingested by 54 mg of mites (the mite biomass in an average square meter) during a year. Caloric values of 3713 and 3999 calories per gram for the puff ball (*Astreus hygrometricus*) cortex were obtained by bomb calorimetry during the course of this study. Dried *Leptoloma* leaves gave values of 3825-4248 calories per gram. These figures agree with those compiled by Golley for the caloric values of plant material. Values for seeds in Golley's compilation, however, ran higher, ranging up to 6000 calories per gram.

An estimated 7686 calories are egested annually by the oribatid population. This figure was obtained by using the 30% egestion estimate and the same monthly factor and caloric values used in calculating ingestion rates above. If the animals assimilate 8% of their body weight per day, they will assimilate about 2058 calories each year, or 20% of the food ingested. Of these 2058 calories, 1965 are used in respiration.

Life cycle data become essential if we are to make estimates of the energies lost to the population through mortality. The complete life history of one oribatid mite, *Oppia nova*, was observed. In culture both adults and young fed upon yeasts and fungal mycelia. At 24° C the egg stage lasted 6-8 days, the larval instar lasted 8-9 days, first nymphal instar lasted 4-5 days, and the second nymphal instar 7-8 days. From the time of oviposition to the time of the emergence of the adult took 25-30 days. There was a 15-day maturation period before the adult laid its first egg; therefore, the minimum generation time would be 45 days. The adults lay about 1 egg every 7-10 days. This rate was obtained from a culture of several individuals which were allowed to oviposit for several days. The culture included both male and female individuals and the total number of eggs was averaged for the total number of individuals; therefore, 1 egg per 10 days per individual is an average population rate.

The long generation time and field data on the fluctuation of populations support the hypothesis that the oribatids completely replace their population once, or at the most twice each year if, as seems likely, reproduction is limited to the warmer months. If a yearly turnover rate is assumed, then 54 mg of mites, equal to 270 gram calories, will go to the next trophic level as dead adults. Adults, however, are not the only individuals which die in the course of the year, and in fact, the young are extremely vulnerable to predators. In culture, for example, the hard-bodied adults are almost ignored by predaceous mites and beetles, while the soft-bodied immature stages are attacked vigorously. Some estimate of the mortality of immature individuals must be attempted before the energy picture of the oribatids is complete. It has already been observed that the adults of *Oppia nova* lay, on the average, 1 egg every 10 days. The egg is about 3% of the body weight of the adult (Table 5). In an attempt to

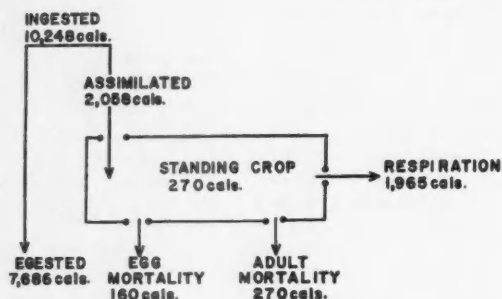
define the length of the breeding period, the cleared, mounted specimens were scrutinized for the presence of eggs in the uteri. Eggs were found in the uteri of specimens captured in April, 1958 through late November of that same year. One individual captured in early December had a gravid uterus. On the basis of these observations a 6-month reproductive period is proposed. Eighteen eggs, then, will be produced each year by a single adult. In a state of population equilibrium, 1 egg must survive to replace the adult which produced it. Therefore, 17 eggs will die in some stage of the life cycle. Mortality from predation is probably heaviest in the larval instar.

TABLE 5. Relationship of egg weight to adult weight in selected mites.

Species category	AVERAGE WEIGHT DETERMINED BY REGRESSION				Egg wt as % adult wt
	Egg wt μ g	s	Adult wt μ g	s	
<i>Tyroglyphus linteri</i>	.085	.0068	1.750	.093	4.9
Oribatid-102	.174	.0180	4.423	.521	3.9
Oribatid-109	.187	.0570	9.34	—	2.0
Oribatid-110	.185	.0000	7.28	—	2.5
Oribatid-111	.337	.1880	12.52	—	2.7
Oribatid-114	.204	—	9.16	—	2.2
<i>Oppia nova</i>	.080	—	1.77	—	4.5
				Avg. Oribatid Acarid	3.0% 5.0%

The actual caloric value of the eggs is unknown; however, these structures are undoubtedly supplied with a quantity of "yolk" material which is in the form of fats and oils. The fat-laden fourth instar larva of *Tenebrio* yielded a caloric value of 6000 gram calories per gram, and this value was arbitrarily used for the caloric value of the mite eggs. The resulting quantity of energy passing out of the population in the form of dead "young" is therefore about 160 calories per year.

The caloric balance sheet for the oribatid biomass in an average square meter for 1 year may be summarized as follows: ingested—10,248 calories; egested—7,686 calories, or 75% of the ingested material; assimilated—2,058 calories, or 20% of the ingested material; respired—1,965 calories, or 96% of the assimilated calories; adult mortality—270 calories, or 13% of the assimilated calories; egg (young) mortality—160 calories, or 7.8% of the assimilated calories. Ninety-five % of the ingested calories has been accounted for in the number of calories egested and assimilated. Five %, or 504 calories, is unaccounted for; this is within the range of experimental error. One hundred and seventeen % of the assimilated calories is accounted for in respiration and total mortality, resulting in a surplus of 17% or 337 calories. Each figure was attained independently from various experimental and field data; none was derived from working only with "known" figures



7,686 + 2,058 = 9,744 (504 CALS. UNACCOUNTED FOR)
1,965 + 270 + 160 = 2395 (337 CALS. OVERESTIMATED)

FIG. 3. Annual energy balance sheet for the oribatid mites found on a square meter of an abandoned field in Michigan, 1958. The arrows indicate the direction of energy flow. The rectangle represents the proto-plasm of the oribatid population.

and solving for "unknowns". Hence, though there are arithmetical discrepancies, each estimate is a fairly close one, and all are supported by combined field and laboratory data. The caloric balance data are also summarized in Fig. 3.

CHANGES IN SPECIES COMPOSITION

When this study was originally undertaken, it was hoped that the extensive collecting data of Hairston & Byers could be employed in a complete analysis of the energetics of the soil fauna. After careful comparison of the 1949-50 fauna and the 1958 fauna, it became clear that the oribatid mite populations had undergone a radical change in the years between 1950 and 1958. This change affected not only the species composition of the upland field, but also the biomass and respiration energies of the oribatid mites involved.

An analysis of the oribatid species composition of the field for the years 1949-50 and 1958 showed that only 5 species were common to the field during both samplings. Twenty-three species categories disappeared from the field after 1950 and were replaced by 19 new species. Numbers of individuals showed a similar decrease, since 33% fewer individuals were found per square meter in 1958. An analysis of the 5 species categories is made in Table 6. It is evident that 2 species have increased their numbers and biomass, 2 have decreased in numbers and biomass, and 1 has remained at about the same level. In spite of the decrease in the total numbers of individuals, there has been doubling of the biomass over the 1950 figure, and a near doubling of the respiration rate (Table 7). The increase in the biomass could be accounted for by the fact that the average individual in 1958 was heavier than the average individual of 1949-50; this is illustrated in Table 8, where an analysis is made of the portion of

TABLE 6. Comparison of the five species categories common to the old field in the years 1949-1950 and 1958.

SPECIES CODE NUMBER		NO. OF IND./M ²		BIOMASS IN MG./M ²		Population trend
'49-'50	'58	'49-'50	'58	'49-'50	'58	
5	120	6410.3	6954.8	1.733	2.436	+
6	105	3449.9	17210.9	2.471	12.019	+
7	115	46.6	16.0	0.311	0.074	-
9	128	21173.3	6890.8	3.815	2.147	-
10	109	170.9	448.7	0.956	1.090	+

+ represents an increase from 1950 to 1958.
- represents a decrease from 1950 to 1958.

TABLE 7. Comparison of various population characteristics of the oribatid mites in the top 12.5 cm of one square meter of the old field for the years 1949-1950 and 1958.

Characteristic	Years '49-'50	Year 1958	% increase (+) or decrease (-) '58 over '50
Total number of individuals.....	87449.20	58293.10	- 33.2
Total biomass in mgs.....	26.96	53.88	+100.0
Total standing crop in calories.....	134.75	269.48	+100.0
Respiration in μ l's per total population per day.....	1843.25	3423.59	+ 92.0
Gm. cal. burned per day per total pop.....	8.85	16.52	+ 92.0
Gm. cal. per year per population....	1052.82	1965.24	+ 92.0

TABLE 8. Comparison of the biomass and weight of individual oribatid mites from the old field for the years 1949-1950 and 1958.

Weight of individuals μ g	BIOMASS '49-'50		BIOMASS 1958	
	mg/m ²	%	mg/m ²	%
.1 and below.....	2.857	10.6	0.000	0.0
.1-.49.....	9.564	35.5	7.900	14.7
.5-.99.....	2.615	9.7	13.958	25.9
1.0-4.99.....	1.661	6.2	14.558	27.0
5.0-9.99.....	7.856	29.1	12.148	22.5
10.0-14.99.....	2.409	8.9	1.923	3.6
15.0 and greater.....	0.000	0.0	3.397	6.3
Total.....	26.962	100.0	53.884	100.0

the total biomass contributed by individuals of various weight categories. Individuals in the .1-.49 and 5.0-9.9 microgram categories make up the greater part of the 1950 biomass, while the .5 through 9.9 microgram classes make up the greater proportion of the 1958 biomass. The milligram per square meter figures indicated that a greater number of heavier individuals produced the greater biomass in the 1958 samples. Apparently, the lighter species of 1949-50 have been replaced by heavier species in 1958.

It is evident then, that over this 8-year period, the oribatid populations have not been in a state of equilibrium, but have been undergoing marked change. The species present on the field during 1949-50 have disappeared, presenting certain difficulties in reconstructing the energy flow picture at that time. Nevertheless, a reasonable approximation of this energy flow system can be reached by studying the slides of the animals and using the area-weight equation and the weight-respiration equation.

The increase in oribatid biomass does not necessarily mean that the rest of the soil fauna has also increased. Evidence from 3 samples from the 1958 field in which all the animals were counted indicates that other groups have declined in numbers of species and numbers of individuals. There were no new species of eupodids and Collembola, but many of the species collected in 1949 and 1950 had disappeared. The implication is that the oribatids have replaced some of the other herbivores found in the old field soil.

It is possible that these drastic changes in the oribatid populations were correlated with corresponding changes in the above-ground system. The component of the latter most likely to exhibit significant modification is the vegetation. The plant cover of the old field was surveyed by Evans & Cain (1952) during the 1949-50 season; they recorded a total of 92 vascular plant species and an average of 148.2 g of air-dried vegetation per m². No formal plant investigation was undertaken in 1958, but clip-plot studies made in July of that year by U. N. Lanham (personal communication) yielded an average of 119.2 g of air-dried vegetation, and casual observations indicated that the same species reported by Evans & Cain and by Evans & Dahl (1954) were still present. That old-field production may remain fairly constant over a considerable period of time is also suggested by Odum's (1960) 6-yr study of abandoned fields on the Savannah River, Georgia, in which the net production underwent no significant change despite considerable alteration in species composition. Such evidence as is available, then, indicates that there has been no radical change in the old-field vegetation to correlate with changes in the oribatid populations.

TROPHIC EFFICIENCIES

In theory the radiant energy taken up by a community is eventually given off as heat or respiration. If one could measure the total energy utilized by a particular community, one could use this as a basis for the comparison of communities. All too often, however, a total energy measurement is impractical, and therefore Lindeman (1942) proposed a series of efficiencies by which the various trophic levels within the community may be evaluated. These efficiencies have been summarized by Patten (1959: 227). The efficiency which is probably the most significant for use in the comparison of trophic levels of different communities is called the "efficiency

of transfer of ingested energy" by Patten and the "ecological efficiency" by Slobodkin (1960). For the purposes of the present study this efficiency is defined as the ratio of the calories ingested by the carnivore level to the number of calories ingested by the herbivore level:

$$EF = \frac{\text{cals. ingested by carnivore}}{\text{cals. ingested by herbivore}} \times 100$$

The population figures of Hairston & Byers were used to obtain the data needed for the efficiency equation. The numbers of individuals listed in Table 1 of Hairston & Byers were averaged, and then extrapolated to numbers of individuals per square meter. (In this case the depth of the square meter is 20.8 cm, rather than the 12.5 cm used by the present author in his study of the oribatid mite populations.) The mounted individuals were measured, and weight and oxygen consumptions were estimated by means of the regression equations.

It is evident that some of the animals found in the Hairston & Byers samples are not members of the soil community: e.g. thrips, true bugs, etc. Indeed, the classification of animals as members of the soil community presented several problems. Many animals appear to belong to the soil fauna but in actuality may not. The ants, carabid and staphylinid beetles, and dipteran larvae will be used as examples to illustrate this point. The most common ant on the field (*Lasius niger neoniger*) was observed to forage for dead animals, feed upon insects, root secretions and stem aphids (Talbot 1953). Plant material collected consisted of seeds, nectar and flower parts. The ants were parasitized by mites, and preyed upon by spiders, tiger beetles, and the flicker. Even though the ants burrow in the soil, their livelihood comes from the above-ground community, and from an energetics point of view they therefore are best considered part of the above-ground edaphon. The staphylinid and carabid beetles present greater problems, when an attempt is made to assign them to a particular community. In culture they have been observed to feed upon Collembola and mites, as well as upon meal worms, flies, leafhopper nymphs, etc. Occasionally in culture, they have even been observed to feed upon apple and banana (Needham *et al.* 1937)! A similar type of difficulty is presented by the small spiders and fly larvae found on the old field. A great amount of field and laboratory study is needed before these relationships can be resolved. These animals were eliminated from the efficiency analysis because of the lack of quantitative data. It was decided to limit inclusion in the category of soil arthropods to the mites, Collembola, Protura, Symphyla, Pauropoda, and Japygida.

Knowing the food habits of an animal is of prime importance to an analysis of ecological efficiency. The literature on the food habits of the soil arthropods is indeed scant and extremely diffuse. Many times on the basis of one observation of one species a whole family has been assigned a particular food

habit. This practice is deplorable but often leaves no alternative. The group called eupodoid by Hairston & Byers has proved to be a composite including members of the Acaridae, Trombididae and Eupodidae. In many cases the feeding habits of these animals were assigned on the basis of the mouth parts, and they were placed in questionable categories by the present author (Table 9). The japygids,

TABLE 9. Average numbers of individuals, biomass, and respiration of the soil arthropods found on 1 m² x 20.3 cm of the old field in the years 1949-1950.

Category	Average number	Biomass in Mg.	Standing Crop Energy Gm. cal.	Resp. in cal.	Food habits
ACARINA					
Parasitoid.....	12414.8	9.330	46.650	354.37	Carn.
Oribatid.....	87582.6	28.596	142.980	115.96	Herb.
Sarcoptoid.....	4721.8	3.466	17.330	138.66	Herb.
Trombidoid.....	1797.8	1.722	8.610	53.33	Carn.
Eupodoid.....	9191.0	3.262	16.310	136.42	Herb.
	20396.4	5.204	26.025	233.32	Herb.?
	2543.0	1.974	9.870	67.06	Carn.
	236.4	0.042	0.210	2.57	Carn.?
Paupoda.....	679.9	0.244	1.220	10.73	Herb.
Symphyla.....	51.3	0.418	2.090	11.52	Herb.
Protura.....	662.1	2.387	11.935	66.53	Herb.
INSECTA					
Japygida.....	388.5	13.472	67.365	298.78	???
Podurid.....	7764.2	7.534	37.670	274.81	Herb.
Entomobryid.....	243.2	2.095	10.475	53.60	Herb.
Sminthurid.....	175.7	0.121	0.605	3.64	Herb.

which make up a considerable portion of the energy and biomass of the field soil arthropods, gave the most trouble. There is one citation in the literature given by Kühnelt in *Soil Zoology* (Kevan ed. 1955) in which he states that japygids are predators; however, intestinal analysis revealed both plant and animal substances. When observed in the laboratory during this investigation these animals huddled in cracks and crevices of the culture jars and slowly died off. They were never observed to feed. For this reason 3 separate analyses were made of the total data: 1), considering the japygids as herbivores; 2), considering them as carnivores; and 3), omitting the group entirely (Table 10).

As indicated above, ecological efficiency can be calculated if the numbers of calories ingested by both the herbivores and carnivores are known. Since feeding experiments were not carried out on the carnivores, the ingestion rates of these animals are not known. Nevertheless, an estimate of the calories involved can be obtained in the following way: if a steady-state condition is assumed, the respiration of the population plus the egestion-excretion of the population will equal the calories ingested. If the population is being preyed upon, then the calories respired and egested-excreted by the predators represent a portion of the ingested calories of the prey population. Therefore, these calories must be included with the egestion and respiration calories of the prey population. Assimilation rates vary with

TABLE 10. Ecological efficiency of the soil herbivores of the old field.

ASSIMILATION %		EFFICIENCY %		
Carn.	Herb.	Without Japex	Japex Carn.	Japex Herb.
32	32	18.9	27.5	16.9
	25	15.4	22.9	13.7
	14	9.6	14.7	8.5
25	32	23.0	32.7	20.7
	25	18.9	27.5	16.9
	14	12.0	18.1	10.6
14	32	32.9	45.4	30.1
	25	28.1	39.4	25.5
	14	18.9	27.5	16.9

the amount of food available, and since the food level of the soil herbivores is unknown for the field during 1949-1950, efficiencies for several assimilation rates have been calculated (Table 10). Richman found that *Daphnia* assimilated from 14 to 32% of the food ingested, depending upon the food level. The figure of 25% was selected as being a convenient number near the middle of that range. The ecological efficiencies were calculated by the following formula:

$$EF = \frac{Re + Re \left(\frac{100-A'}{A'} \right)}{Rh + Rh \left(\frac{100-A''}{A''} \right)}$$

where Re is the respiration of the carnivore, Rh is the respiration of the herbivore, A' is the % assimilation of the carnivore, A'' is the % assimilation of the herbivore, and EF stands for ecological efficiency. In applying the data of this study to the formula given above, two variables were considered: (1) the assimilation rate of the herbivores and carnivores, and (2) the uncertain feeding status of the japygids. Hence, instead of obtaining a single efficiency, a range of efficiencies resulted from the several possible combinations of the variables.

The number of calories respired by the herbivores was 2045.19 when the japygids were omitted and also when they were included as carnivores, and 2343.97 when the japygids were considered to be herbivores. The numbers of calories respired by the carnivores was 477.33 when the japygids were omitted and also when they were included as herbivores, and 776.10 when the japygids were considered to be carnivores. Thus the total amount of respiration for combined herbivore and carnivore populations was 2522.52 calories when the japygids were omitted from both groups and 2821.30 calories when they were included in either herbivore or carnivore group. The above values are based upon the number of animals found in 1 square meter of soil, 20.8 cm deep, and over a year's period of time. The efficiencies range from 45.5% to 8.5% depending

upon the various assimilation efficiencies proposed for the components of the system and the position of the japygids in the trophic scheme. It will be noted that wherever the assimilation rate for the carnivore and the herbivore is the same, i.e., 32%, 25%, 14%, for each, the EF for that column is the same: i.e., 18.9, 27.5, or 16.9. When A' and A'' in the above equation are equal, EF becomes a ratio of the 2 respiration rates, thereby giving the same efficiency for all assumed assimilations.

Table 11 gives the range of the total calories consumed by the herbivores used in calculating the efficiencies found in Table 10. It will be noted that not only are there different caloric values for the same efficiency, but there are also the same caloric values for different efficiencies. Which value or values are the most reasonable? One approach is to determine how many calories the herbivores can produce over a year's time. Life history information showed that the acarid mites (*Caloglyphus* and *Tyroglyphus*) were capable of 2-3 generations per month (Table 12), and that they could deposit 56-235 eggs per lifetime per female. The oribatids have a lower reproductive rate and longer development time. It was found that the egg weight of

TABLE 11. Caloric consumption and ecological efficiency calculated for the soil herbivores found on the old field during 1949-1950.

Consumption by herbivores cals.	Ecological efficiency %	Consumption by herbivores cals.	Ecological efficiency %
7882.89	18.9	11713.09	45.4
8300.54	23.0	12174.25	28.1
8816.57	27.5	13369.81	25.5
8816.57	16.9	13502.65	39.4
9234.23	20.7	15515.87	9.6
9495.66	32.7	15933.53	12.0
9699.74	15.4	16449.56	14.7
10090.11	18.9	17128.65	18.1
10385.03	32.9	17564.65	8.5
10606.13	22.9	17982.31	10.6
10867.56	13.7	18103.38	18.9
11285.21	16.9	19346.08	27.5
11285.21	27.5	20152.27	16.9
11318.83	30.1		

Tyroglyphus linteri was about 5% of the adult weight (Table 5). Using this information it was calculated that the herbivore population could produce 1928-3390 calories in eggs and adults for the maintenance of the predator populations. Most of the caloric requirements calculated for the carnivores in constructing Table 10 fell between 1260 and 3360 calories. However, the set of "Japex carn." efficiencies calculated at an assimilation level of 14% depended on a value of 5325 calories consumed each year by the carnivores. This value is more than the herbivores can possibly produce during a year, and the dependent set of efficiencies is therefore not a reasonable one.

Another way to try to narrow the choice of the

TABLE 12. Life cycle information of several herbivorous mites.

Genus and species	Length of life	Eggs produced during life	Development time	Reference
<i>Tetranychus telarius</i> ...	20-40 days	70	—	Metcalf & Flint 1939
<i>Tarsonemus pallidus</i> ...	14 days	—	—	Metcalf & Flint 1939
<i>Rhizoglyphus hyacinthi</i> ...	30-60 days	50-100	—	Metcalf & Flint 1939
<i>Rhizoglyphus echinopus</i> ...	17-27 days	—	—	Baker & Wharton 1952
<i>Phyllocoptes oleivorus</i> ...	7-14 days	—	—	Metcalf & Flint 1939
<i>Paratetranychus pilosus</i>	21 days	30-35	—	Metcalf & Flint 1939
<i>Paratetranychus citrii</i> ...	—	—	21- 35 days	Metcalf & Flint 1939
<i>Halotydeus destructor</i> ...	25-50 days	—	—	Baker & Wharton 1952
<i>Caloglyphus mycophagus</i>	18-23 days	235	4-9 days	Rohde 1959
<i>Tyroglyphus linteri</i> ...	32-84 days	56-214	14- 25 days	Engelmann
<i>Oppia nova</i>	—	.12 egg per day	25- 30 days	Engelmann
<i>Pseudotritia</i> sp.....	—	—	56 days (average)	Rohde 1955
<i>Euphthiracarus flavum</i> ...	—	—	60 days	Rohde 1955
<i>Galumna elimatus</i>	—	—	72-107 days	Sengbusch 1954
<i>Galumna nerosus</i>	—	—	45- 50 days	Sengbusch 1954
<i>Galumna longiplume</i> ...	—	—	58- 66 days	Sengbusch 1954

various efficiencies would be to calculate the amount of food material coming into the herbivore population. At the beginning of this study, it was believed that the population of herbivores fed upon the dead plant and animal material of the old field. It soon became evident that this was not so, and that the herbivores were feeding upon the organisms which were attacking the dead material; i.e., the mites were feeding upon the fungi and bacteria, and incidentally upon some of the dead material. If the various ecological efficiencies that were found for the herbivores are assumed to be the same for the bacteria and fungi, the result will be a series of estimated amounts of food available to the mites. The 148 grams of vascular plants which were found on 1 square meter of old field make up the greatest part of the dead material which falls to the decomposers each year. This amount of plant material is equivalent to 620,000 calories. If the lowest EF of 8.5 is used, the result will be an estimated 22,134 calories of fungi and bacteria ingested by the herbivores. This efficiency will adequately fill the needs for all the efficiencies calculated for the soil herbivores (Table 11). However, the 20,152.27 caloric value at 16.9% EF comes the closest to the 22,134 caloric estimate. One must keep in mind that other animals such as nematodes, rotifers, and protozoa also feed upon bacteria and fungi. Nematodes and rotifers were found in the soil of the old field, and it was estimated that the nematodes accounted for only about 360 calories per year. However, this is a very crude estimate, made on the basis of only 1 sampling, and they may consume more. The 16.9% efficiency was obtained by assuming a 14% assimilation rate for both herbivore and carnivore.

In a final attempt to narrow the range of ecological efficiencies the figure of 40% body weight ingested by the oribatid mites was applied to the total biomass of the herbivores. This weight, when con-

verted into calories, gave estimates of 10,150.88 calories consumed when the japygids were omitted and 12,712.74 calories consumed when the japygids were included as herbivores. Using the 2 extremes in assimilation rate for the carnivores (i.e. 14% and 32% assimilation) the following efficiencies were obtained: when the japygids were considered to be herbivores, the ecological efficiency was 8.32%; when the japygids were considered to be carnivores, the ecological efficiency was 12.47%. It can be seen that even with 1 variable—the assimilation efficiency of the predator—the range of possible ecological efficiencies is considerable. The 47% value is once again too high because it required 4,620 calories of ingested herbivore to support the carnivore population, 1230 calories greater than can be produced by the herbivores during the year. Even the 32% efficiency may be too high, for it required 4074 calories to support the carnivores.

At the present stage of knowledge, therefore, any ecological efficiency between 8% and 30% may be considered reasonable for soil herbivores.

DISCUSSION

To create the proper setting for the discussion to follow, the use of the word "community" must be clarified. In most texts the community concept is supported and discussed with such assurance that the reader is led to believe that the concept is a rule in ecology. MacFadyen (1957: 238) points out that "the term community is a shibboleth and a label for a working hypothesis." Therefore, the discussion and re-definition of the term is not out of order. The definition of community used in this paper is as follows: an assemblage of populations coexisting in time and space, mutually regulative and interdependent, and depending ultimately upon some common energy source. This definition contains elements from several sources, principally Allee *et al.* (1949) and MacFadyen (1957). The stipulation about the energy source is lacking in most definitions; yet, it would seem that this requirement is basic to understanding of the community. The food web, if known, can be used to delimit one community from another. A common energy source, however, does not necessarily have to be solar radiation, but can be another form of energy, such as organic materials of various kinds, or even various simple chemical compounds which are capable of being broken down by microorganisms (e.g., sulphur and iron bacteria).

If there is a basic trophic scheme for all communities, then the energy relationships should be reflected in the community structure. Community structure has been approached from several points of view. Physical description came first, but this approach cannot be tested by the application of mathematical processes, and thus relies solely upon the acuity of the observer. Hairston (1955) has summarized another line of approach, that of comparing species abundance with mathematical models. Of all the models used, the ones by MacArthur (1957) are most appealing because they are based upon

biological principles rather than upon some theoretical mathematical curve. Data of relative species abundance best fit the MacArthur model which assumes that the niches are continuous but not overlapping. When the number of individuals per species (relative abundance) is plotted against the predicted curve, however, biological data do not fall along the predicted curve. Hairston attributed this difference between observed and expected plots to the fact that niche size is not determined randomly as suggested by MacArthur's model, but rather, niche size is a function of an organized system—the community. Hairston further pointed out that food is the one constituent of the community that will fit this model. Since, in all analyses mentioned by Hairston, numbers of individuals were used, it is possible to plot an energy function of these animals as related to their food (i.e., calories respired) against the theoretical curve. Figs. 4, 5, and 6 show the form of the observed data with respect to the predicted curves when numbers of individuals, biomass, and calories respired for a year are plotted for the oribatid mites found on the old-field in 1958. The observed curve for numbers of individuals is similar to those presented by Hairston (1959). Biomass gives a smoother curve, with a shape similar to that of the predicted curve, but still exhibiting the same

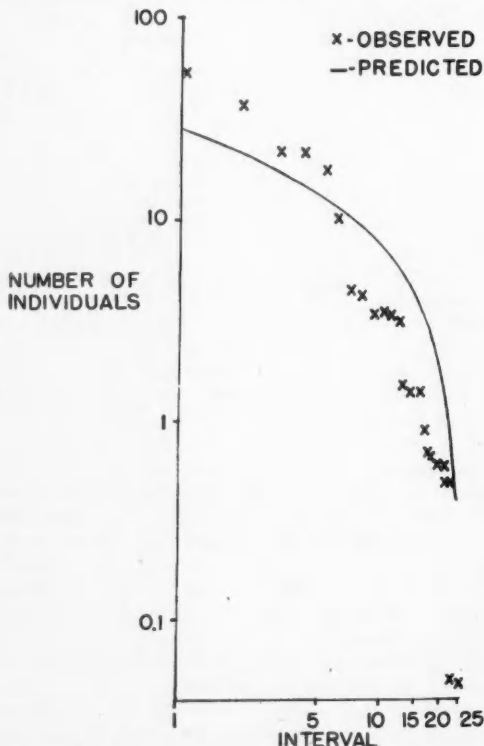


FIG. 4. Number of individuals of each species of oribatid mite found on the old field in 1958, compared with the model of MacArthur.

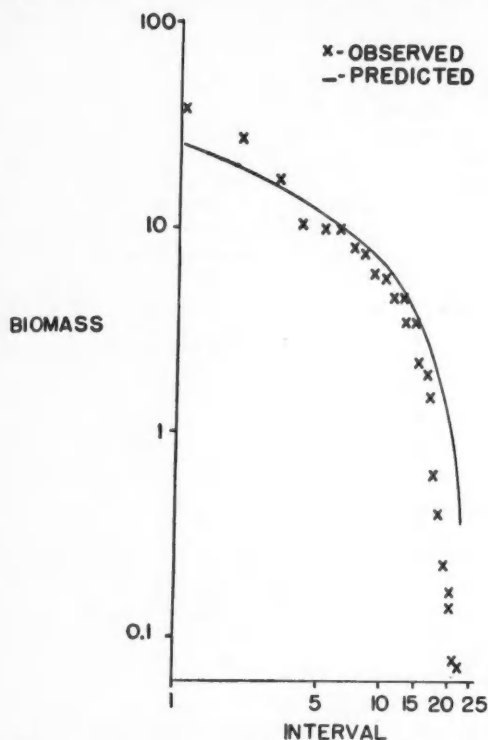


FIG. 5. Total biomass of each species of oribatid mite found on the old field in 1958, compared with the model of MacArthur.

distortions as did the previous curve. When respiration calories are plotted, the top half of the curve conforms to prediction, but the bottom half of the curve still falls away. This curve could be interpreted as meaning that the common organisms fit the model and have their niche size determined in a random manner, while the rare individuals do not fit the model and do not have their niche size determined at random. However, when the respirations for all of the soil arthropods found on the old field during 1949 and 1950 were plotted, the curve still showed the deviations of the plot for numbers of individuals. This may reflect the fact that several trophic levels are included in the total analysis of arthropods, while only part of one trophic level was considered in the analysis of the oribatids. It seems that for a single trophic level, at least, energy units more nearly fit the predicted curves. There is indication, then, that Hairston's assumption has validity and that the niche or status of an animal in the community might therefore be defined in terms of the amount and kind of food it eats, hence ultimately in terms of energy consumed.

The food web of the community is one of the more important concepts of community organization, and its complete qualitative and quantitative description should be the ultimate goal of the community ecologist.

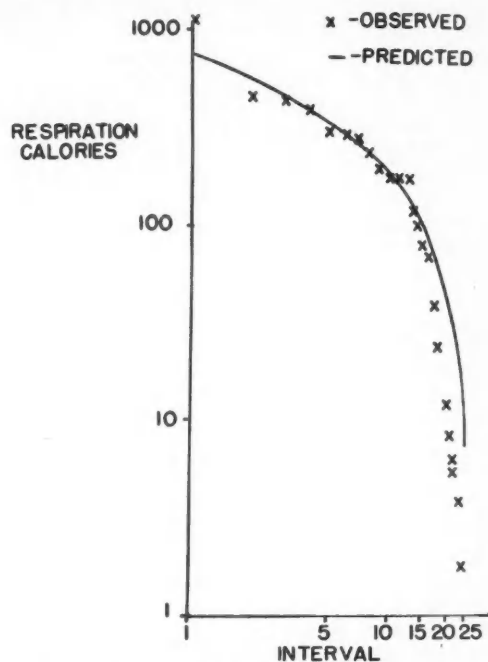


FIG. 6. Total respiration of each species of oribatid mite found on the old field in 1958, compared with the model of MacArthur.

ogist. The food web of the soil community is poorly understood. The role of the soil arthropods in this food web will be considered next, because these organisms hold a key position in the soil community.

It is generally accepted that the soil arthropods play an important role in the soil-building process. Allee *et al.* (1949) review the classification of the soil organisms according to their food habits. This classification, based mostly upon the ideas of Fenton and Jacot, divided the soil organisms into 5 major groups: 1), chemical agents (bacteria and fungi); 2), ectophagous agents (species which eat whole green leaves and perform some chemical breakdown); 3), endophagous agents (agents which "mine" leaves and roots); 4), predators; and 5), shelterers (animals which use the soil as a retreat only). A common description of the process of soil building is as follows: first, the dead material falls to the ground; then the arthropods grind the material into small bits; and finally the bacteria and fungi attack the "grindings" and break the material down to an elemental state, which can once more be exploited by the plants. Many of the observations on food habits of soil arthropods seem to support this view. When van der Drift (1950) fed millipeds very moist leaf litter, they assimilated about 6% of the material. Gere (1956) fed millipeds as well as isopods on litter. He noted however, that the animals did much better on the litter from the Fx layer, or decomposed material just above the mineral soil, than

they did on the newly fallen dead leaves. Wallwork (1958) and Rohde (1955) raised and maintained oribatid mites on leaf litter or decayed wood. Birch & Clark (1953) report Riha as stating that the oribatids feed upon wet dead leaves, wet dead wood, and that two species feed upon fungal mycelia.

In this study, however, the soil arthropods would not culture upon fresh dead, or dried plant material, even after it was wetted. Green plant material did not seem acceptable. *Oppia nova* was finally cultured on yeast. It was observed then that several other species of oribatid mites (family Eremaeidae) fed upon yeast, (*Saccharomyces cerevisiae*), mushrooms (*Mycena fibula*, *Agaricus campestris* and others) and the hyphae of *Aspergillus inornata*. A belbid mite specialized upon a mold (an imperfect) which grew upon decaying arthropod muscles. The particular fungus was very sticky and smaller mites would become trapped if they tried to cross it, but the long-legged belbid had no such difficulty and fed exclusively upon this mold in culture. Further search of the literature disclosed observations similar to those cited above. Van der Drift (1950) cites Dr. Rooseboom's observation that *Oppia neerlandica*, *Oribatula tibialis*, *Chamobates schultze*, and *Galumna cf. dorsalis* all fed upon molds. Wallwork (1958) found fungal mycelia in the guts of most of the mites that he inspected. The guts were also filled with other material. Sengbusch found that the young of *Galumna* (several species) would feed on the alga *Protococcus*, while the adult fed upon moss. Rohde (1959) raised the mite *Caloglyphus* on fresh hamburger, and the same mite was cultured by D. Pimentel (personal communications) on *Neurospora*. Metcalf & Flint (1939) review the life histories of several mites which are pests on agricultural plants. Representatives of the same families including the agricultural pests are found in the soil of the old field. Finally, the volume edited and compiled by Needham *et al.* (1937) gives numerous culture methods of invertebrates. The food recommended for the milliped *Euryurus erythropygus* is moist decayed sapwood; for oribatids, and tyroglyphids, lichen, mosses, cheese mold, and moist dead wood. The mushroom mite, *Tyroglyphus linteri*, various Collembola (*Achorutes armatus*, *Proisotoma minuta*, *Lipidocyrtus cyaneus*, *L. albus*, and *Sminthurus caecus*), Diptera larva (*Sciara coprophila*, *Neosciara pauciseta*, *Calliceras* sp., and members of the *Cecidomyiidae*) have all been raised on commercial mushroom spawn. Yeast has been used to culture *Proisotoma minuta* (Auerbach *et al.* 1957), and *Tyroglyphus linteri* (present author). Similar references on the food habits of soil-dwelling arthropods may be found in the work of Cloudsley-Thompson (1958), and Kevan (1955).

The question raised here is, do soil arthropods actually feed upon dead material, as has been so often reported, or are these animals actually deriving their nourishment from mycelia of fungi within the decaying litter? The definition of the word "feed" in the above question creates the problem, because

an animal may ingest material and yet not be able to assimilate it. The majority of the dead matter falling to the floor stratum of a community is in the form of plant material, most of which is cellulose and hemicellulose. The starches and sugars contained in the living leaves of the plant have undoubtedly been used up by the cells of the plant as the leaves died, have been transported to other parts of the plant for storage, or have been leached from the leaf or oxidized before the leaf fell to the ground. Therefore, an organism must have cellulase in order to break down the cellulose for use as a food source. The lower plants (bacteria and fungi) are well-supplied with cellulase, as are many of the parasitic protozoa. However, when the metazoa are surveyed for the presence of cellulase (Prosser *et al.* 1950) it is found only in various Mollusca and the earthworm (*Lumbricus*). Symbiotic bacteria and/or protozoa are the usual source of cellulase in most wood-eating insects. Brues (1946) has shown dramatically the dependence of insects upon microorganisms. Using the fruit fly as an example, he points out that although the larvae appear to be feeding upon the banana medium, they are actually feeding upon yeasts growing in the medium. If the culture is kept completely sterile, the fly larvae die. In the same line, a soil arthropod may be ingesting dead plant material; however, it is digesting the living bodies of the fungal hyphae which are attacking the dead material. In each case where the food habits of a soil arthropod have been explored fully, it has been shown that fungus is a suitable food material. It is possible that the soil arthropods possess cellulase, but in view of the lack of the enzyme in the rest of the Metazoa, this possibility seems to be slight. Some soil arthropods may, of course, have intestinal symbionts. Rohde (1955) reports that the young of the box mite (*Pseudotritia* sp.) consume the feces of the adult, and that the adult's digestive tract is filled with rod-shaped bacteria. This feces-eating habit is common of other wood-feeding arthropods such as the passalid beetles and termites. New enzymes for the soil arthropods do not have to be postulated however, to allow for the break down of the dead plant material in the soil community. The bacteria and fungi already possess the necessary cellulases. These plants digest their food extracellularly and then absorb the dissolved sugars. An arthropod feeding upon the dead material, then, has access to the sugars digested by the fungus as well as to the fungal protoplasm. In culture glucose crystals were fed upon by galumnid and eremaeid mites, indicating that these animals were attracted to sugars.

Not all of the soil arthropods are herbivores; some are known to be carnivorous. All of the Parasitidae and Trombididae feed upon mites and Collembola or are parasitic upon vertebrates and large insects. These animals presumably act as population controls on the herbivores or upon the animals which they parasitize.

This review of the feeding habits of the soil arthropods, and especially of the food preferences of the mites, suggests that the traditional role of these animals in the soil community needs some revision. It follows from the above observations that the role of the soil arthropods is not merely that of a grinding mill. Rather, they form a control mechanism upon the fungus populations. The soil arthropods affect the fungi in at least three different ways. First, the arthropods feed directly upon fungi, thereby cutting the biomass of the plants in the immediate area. In this sense the arthropods act as a depressing factor upon the fungal population. Secondly the arthropods clear away material penetrated by hyphae, exposing new material to the action of the fungi. The oribatid mites also have a third important effect upon the fungi, since they defecate while they are feeding. The feces of these animals are usually filled with spores from some previous meal. The mite feces then inoculate newly-exposed material with new fungal spores. This action tends to accelerate the breakdown of the material in the immediate area, for it is known that the respiration of a rapidly growing fungus colony is greater than that of a mature colony (James 1953). Finally, of course, there is a certain amount of grinding or reduction of particle size in the feeding process, as well as the seeding of the feces with microorganisms. The reduction of particle size would seem more important for the bacteria, which can work only on the surfaces of materials, than for the fungi, which are capable of penetrating materials.

This analysis of community energetics further suggests that soil arthropods do not fit precisely into Lindeman's original scheme, or at least that they have not been properly elaborated upon in that scheme. A schematic representation of the energy flow of the old field is given in Fig. 7. Lindeman's symbols are retained in the interest of standardization and clarity. For each trophic level (capital lambda) there is a flow of energy into the level (small lambda) in the form of food or radiation depending upon the level, and the energy leaves that level in the form of respiration (R), decomposition (D), and energy consumed by the next level (small lambda). Each level is given a number: 1 for the green plants, 2 for the herbivores, 3, primary carnivores, and so forth. In the Lindeman scheme the "D" of decomposition of the trophic level either embraces the whole soil fauna, or it includes only the bacteria and fungi, thereby omitting the herbivores and carnivores which are directly dependent upon these plants for food. In the present modification of the scheme, the soil complex is represented by the double numbers: 11 for the fungi and bacteria, 22 for the herbivorous mites, Collembola, round worms, etc., and 33 for the carnivorous mites.

This trophic diagram of the old field indicates 2 major flows of energy, one above-ground and the other one in the soil. The above-ground system is powered directly by the sun's energy, captured by the green plants, while the soil system is powered

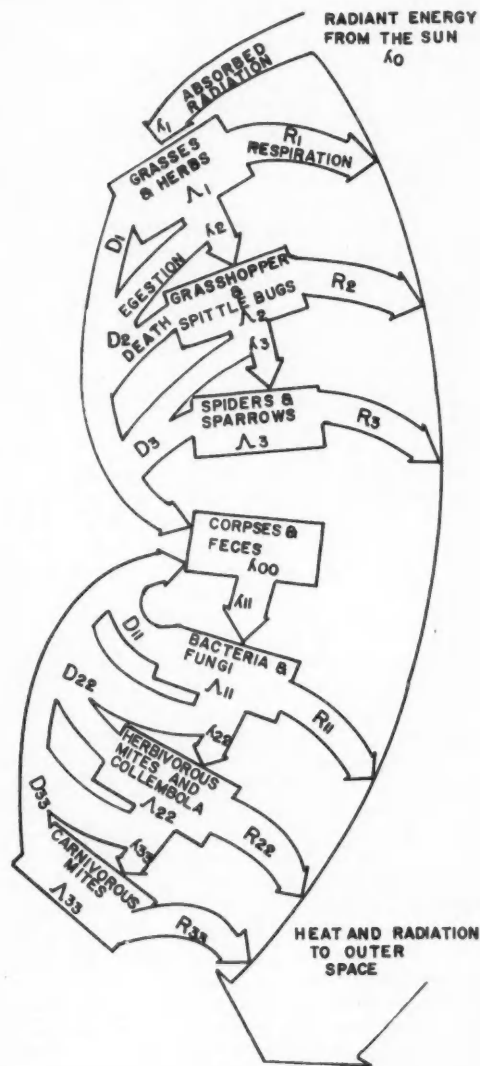


FIG. 7. A schematic energy flow diagram for the upland of an old field in Michigan. The symbols used are those of Lindeman. Note that "D" represents decomposition; this includes egestion, which has never become part of the protoplasm of the population, and death, which has been part of the protoplasm of the population.

directly by the dead bodies and feces of the above-ground members. The dead material, of course, was originally produced by the green plants. The soil plants can be placed in trophic levels equivalent to those of the above-ground system, and given a supply of energy, the soil system will continue to operate. The fact that the oribatid population underwent such a complete change, while the above-

ground community changed little, tends to support the idea that the soil system is a separate community from the above-ground community. The surface of the soil then becomes an ecotone and animals such as spiders, staphylinids, and carabids can be considered ecotonal animals. These facts support the views of Birch & Clark (1953) that the soil is an ecological community in its own right.

The diagram depicts the energy flow of the old field only in its broadest outlines and is admittedly an over-simplification of the true picture. A single animal may not fall into a single trophic level, or may change food habits according to season: e.g., the chipping sparrow, which feeds mostly upon arthropods during the breeding season and mostly upon plant seeds during the rest of the summer. Imports and exports have also been ignored. In the old field, for example, windborne seeds and flying arthropods, are continually emigrating or immigrating. Rains leach materials from the soils. Carnivores often feed from several different trophic levels, thus complicating the picture further. Without information on these unknowns, the scheme is probably best left in simplified form.

A value of the Lindeman scheme is that it will allow the comparison of communities at all levels. At present this comparison is fairly rough because of imperfect methods of collecting needed data. On the population level the results for the oribatids compare favorably with those of Richman (1958) and Slobodkin (1959) for *Daphnia*, the water flea. The only outstanding difference between the two kinds of organisms involves the amount of energy put into reproduction by the populations. The *Daphnia* have a high reproductive rate, while the oribatids have a low rate. Assimilation rates and respiration vs. growth calories for non-reproductive adults of *Daphnia* and *Oppia* are all in the same range. Richman has shown that the growth rates and assimilation rates of *Daphnia* are similar to those found for other animals including vertebrates. He reiterates that the basic biochemistry of all animals is very similar. When the ecological efficiency of the soil arthropods is compared with that of organisms in aquatic communities, the efficiencies also fall in the same range. The ecological efficiencies for the herbivores of several fresh water communities are summarized by Patten (1959). These efficiencies range from 5.5% to 21.0%. From the numerous efficiencies found for the soil arthropods it appears that anything from 8.5% to 30% would be a reasonable estimate. It may disturb some persons to have the ecological efficiency rating so variable. If one considers the efficiency of a population at monthly intervals, it will be seen that there are fluctuations which reflect food levels and predator levels. The overall yearly estimate, then, is an average of the population's efficiencies over the 12-month period. When food supply is abundant, per cent assimilation is low and more calories are "wasted" (defecated) by the population. At the other extreme, when food is scarce, greater amounts of food are

assimilated and less is wasted. The ecological efficiency is variable just as a respiration rate is variable, but it should vary within a limited range. Slobodkin (1960) believes 5-15% to be the reasonable limits of this range. However, the data for the soil arthropods suggest that the upper limit may be 20% or higher.

Another efficiency that is a valuable tool in the comparison of several communities is the "efficiency of transfer to each level in terms of original input" (Patten 1959). If the above-ground system and the soil system are considered to be a single community, the primary energy source for the community, is, of course, the sun. The calculated efficiency of transfer of solar energy to the herbivore level of the soil arthropods is .02-.03%. The reason for such a low efficiency is that the soil arthropods are at least 3 trophic levels away from the original energy source. If, however, we consider the soil system to be a separate community, then the energy source and original input for the community is the amount of dead material available. This places the soil herbivores on a par with the above-ground herbivores with respect of trophic level within their communities. The efficiency of transfer thus calculated for the trophic level of the soil arthropods is in this instance 1.5-2.0%. Patten's summarized values for the efficiency of transfer to the herbivore level in aquatic communities ranged from .05 to 6.8%. The efficiency values for the soil arthropods fall well within this range.

In short, these data on the efficiencies of the soil arthropods, both at the population level and at the trophic level, lend support to the hypothesis that all communities function according to the same energetic principles.

SUMMARY

1. In 1958 a field sampling program and laboratory studies were undertaken with the soil arthropods of an old field in south-eastern Michigan to elucidate the energy dynamics of the soil system. Laboratory methods involved Tullgren extraction, biomass determination, respiration studies and calorimetry.
2. An energy balance sheet was drawn up for the oribatid mites. It was calculated that these mites in 1 square meter 12.5 cm deep consumed 10,248 calories of food each year and assimilated 2,058 calories or 20% of the food ingested. Respiration accounted for 96%, and mortality for 20% of the assimilated material. The error for the calculation was 13%.
3. When comparison was made with the data obtained by Hairston & Byers (1954) on the same field, it was found that the oribatid mite populations had changed markedly. The species composition had changed completely save for 5 species. Numbers of individuals had decreased 33% between 1950 and 1958, but the biomass and calories of respiration had doubled or almost so. It is suggested that the oribatid fauna has probably

- displaced other components of the soil, and that the total arthropod biomass has remained at a constant level.
4. The ecological efficiency was calculated for the soil arthropods. Due to the lack of certain feeding information, reasonable efficiencies ranged from 8% to 30% for the soil herbivores.
 5. When energy units (respiration calories) were used in place of numbers of individuals in one of MacArthur's models, the observed curves more nearly fit the predicted curves, lending support to the idea that the niche is the amount and kind of food a population consumes.
 6. The main role of the soil herbivores was found to be that of controlling the fungal and bacterial populations which are breaking down the dead materials. These arthropods can both accelerate and retard the growth of the decay organisms. The soil carnivores serve as population controls on the herbivores.
 7. The soil system is considered for two reasons to be a community separate from the above-ground system. First, it has a trophic level system similar to that of the above-ground system, and secondly, changes in species composition in the soil arthropods are apparently independent of changes in the above-ground system.
 8. Data on *Daphnia pulex*, the water flea, and *Oppia nova*, an oribatid mite, compared favorably with respect to their respiration and assimilation efficiencies. The range of ecological efficiencies (8.5-30%) for the soil herbivores compared favorably with ecological efficiencies for the same trophic level in the aquatic communities, and the 1.5-2.0% efficiency of transfer to each level in the soil community also fell within the range of efficiencies found for the aquatic communities. These data lend support to the hypothesis that all communities operate on the same energetic principles.
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THE FAUNA OF OYSTER BEDS, WITH SPECIAL REFERENCE TO THE SALINITY FACTOR

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TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	239	DISTRIBUTION	249
Description of Beaufort Area	240	Seasonal Succession	250
The Oyster Population	241	Number of Species	251
PHYSICAL FACTORS	241	Effect of Hurricanes	253
Salinity	242	Individual Species	255
Temperature	243	SALINITY TOLERANCE	257
Hydrogen Ion Concentration	244	Methods	257
Color	244	Results	258
Turbidity	245	DISCUSSION	260
Current	245	SUMMARY	263
COLLECTION STATIONS AND METHODS	245	LITERATURE CITED	263
FAUNAL COMPOSITION	246		

INTRODUCTION

Jones (1950) pointed out three prime factors in the distribution of marine organisms: temperature, substrate, and salinity. Temperature is generally recognized as being the principal factor in determining the extent of the great marine biogeographic realms or provinces (Ekman 1953, Hutchins 1947). Within each realm, province, or subprovince, the substrate largely determines the nature of the community of organisms that lives on and in it (Thorson 1955). Salinity becomes an important factor in estuarine areas, where fresh waters flow into and mix with seawater.

In recognition of the importance of salinity in the estuarine environment, Redeke (1932) partitioned estuarine waters into salinity zones which correspond with the distribution of estuarine animals. The fauna of the broad zone of brackish water in an estuary is composed primarily of species of marine origin (Percival 1929). From a familiarity with both the invertebrate and fish fauna of the Texas coastal region, Gunter (1950) stated: "The fauna of brackish waters is marine and is not derived from fresh water. As the waters become fresher along the salinity gradient, certain invertebrates that cannot tolerate lowered salinities drop out of the picture, but others persist. There is no compensating increase in the number of species by invasion of species from fresh water and therefore the number of species in waters of low salinity is low, but those present are marine."

What factor is responsible for limiting the distribution of these species? Observations of natural distribution suggest that salinity is generally the

limiting factor (Redeke 1932, Ladd 1951, and others). However, some other factors may serve to limit their distribution, such as availability of food, predation and competition of other species, sensitivity to temperature changes, and associations with particular bottom types.

Many so-called estuarine species have a wide ecological range and may endure the salinity of ocean waters very well; they thrive especially well in estuarine conditions because species which would compete with them in more saline water cannot endure the lower salinities in estuaries. The eastern oyster, *Crassostrea virginica* (Gmelin), is considered such an estuarine organism because it thrives under estuarine conditions. The abundance of food in estuaries and the inability of many oyster enemies to live in brackish water allow oysters to flourish (Fisher 1948). Whereas oyster beds typically serve as centers for a large and varied fauna that utilizes the hard substrate and protection provided by oyster shells, many upstream beds do exceptionally well because drills, starfish, and boring sponges cannot stand the reduced salinities that prevail there (Korringa 1952). Where oyster beds range far up an estuary, they provide an opportunity to observe the distributional limits of species within this single substrate type, with salinity being the chief variable.

A clear presentation of salinity distribution of oyster associates would show which areas of an estuary are relatively free of predaceous or competing species and are therefore more suitable for commercial oyster culture. For each species the relative tolerance to lowered salinities would provide a basis

for the prediction of distribution should the salinity regime of an area be radically altered, such as by the opening or closing of an inlet. Man-made navigational waterways and severe tropical storms are potential sources of such change. The findings of such a study should contribute toward the prediction of faunal changes accompanying salinity changes and, indirectly, of effects on the productive potential of the oyster industry of the area.

The purpose of this study was to investigate the fauna of the oyster bed community to test the hypothesis that salinity is the primary factor which limits the upstream penetration of the animals of this community. Because of the absence of sufficient information about the environment, the first part of this report presents hydrographic conditions in the Newport River estuary. Next follows a discussion of the fauna of oyster beds in this area. In the third part, the distribution of these species is related to season and salt content of the water. Because three hurricanes provided a natural experiment on tolerance to reduced salinities during the course of this study, observations of their effects on distribution, complementing the normal pattern, are included in this section. In the fourth part, results of salinity tolerance experiments on twenty species of the oyster bed community are presented. When these experimental results are compared to the patterns of distribution treated in preceding sections, they indicate the importance of salinity as a limiting factor.

This report is based on a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy to Duke University. The author wishes to express grateful acknowledgment to Dr. I. E. Gray of the Department of Zoology, under whose direction this study was made, and to Dr. C. G. Bookhout, Director of Duke University Marine Laboratory, who made its facilities available. Two National Science Foundation Awards to Duke Marine Laboratory helped support the study.

DESCRIPTION OF BEAUFORT AREA

The North Carolina coastline contains three cusped capes which project southeastward into the Atlantic Ocean, the most northern and most prominent being Cape Hatteras. The Beaufort area lies at the northern part of the embayment between the two southern capes, Cape Lookout and Cape Fear. At this point, the coastline is formed of low, sandy barrier islands, locally referred to as "outer banks," which are oriented in an east-west position. Opposite the mainland town of Beaufort lies Beaufort Inlet, draining the eastern end of Bogue Sound and the western end of Back Sound (which lie between the barrier islands and the mainland) and North and Newport Rivers (Fig. 1). These rivers are relatively short and regarded by Marshall (1951) as simply arms of the sounds. However, they do exhibit gradients as a result of seepage and runoff from land and, in the case of Newport River, flow from a non-tidal portion lying in the Coastal Plain north and west of

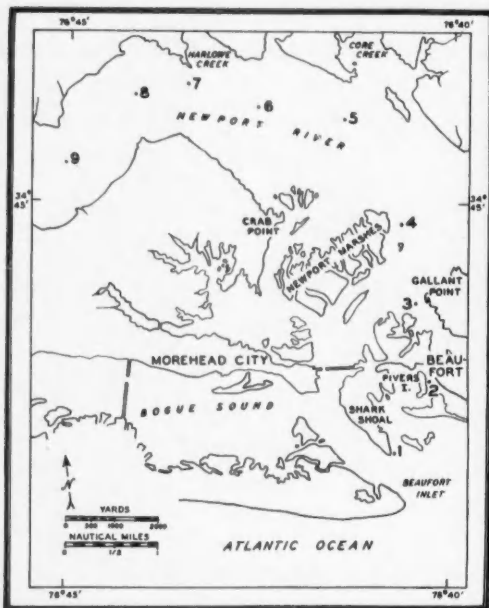


FIG. 1. Chart of the Beaufort (N. C.) area showing the location of hydrographic stations: 1—Shark Shoal, 2—Pivers I., 3—Gallant Point, 4—Newport Marsh, 5—Crab Point, 6—Midway, 7—White Rock, 8—Turtle Rock, 9—Cross Rock.

Beaufort Inlet. Newport River receives the Intra-coastal Waterway through Core Creek Canal, which connects with Pamlico Sound at its northern end. The tidal portion of Newport River extends 5 miles west of Core Creek as a very shallow body of water overlying a soft mud bottom, occasionally interrupted by natural oyster reefs. Low islands of salt marsh and dredge waste occur in the river below Core Creek. Between these islands, two deep channels lead to the inlet, one by Morehead City on the western bank and one by Beaufort on the eastern bank.

This coastline south of Cape Hatteras is included in the Carolinian faunal subprovince, inhabited by many subtropical species which find their northern limit at that point. North of Cape Hatteras lies the Virginian subprovince, inhabited by a temperate fauna which ideally would find its southern limit at Cape Hatteras (Ekman 1953). However, a number of species listed by Stafford (1913) as characteristic of the Virginian subprovince extend south of Cape Hatteras as far as the Beaufort area, 70 miles to the southwest. For that reason, this study includes both species that range northward along the Atlantic coast and species that range southward to Florida and the Gulf of Mexico. In the Beaufort area, they may be collected on the same oyster bed. For example, both *Urosalpinx cinerea*, the principal oyster drill of the Atlantic coast, and *Thais floridana*, the oyster drill of the Gulf coast, are commonly found

on oysters in this area. A rich fauna is present in the Beaufort area, of which many divisions have been treated by taxonomists.

THE OYSTER POPULATION

The eastern oyster is distributed along Newport River from Beaufort Inlet to well above Cross Rock, the upstream limit of this study. Grave (1903) charted the distribution of oyster bottoms in Newport River, showing natural beds occupying 257 acres of bottom. Near the inlet, oyster clusters are found on every hard object in the intertidal zone, such as the rocks of jetties and breakwaters, pilings, and large shells. Such an intertidal distribution is characteristic of oysters near Beaufort Inlet, with only scattered clusters and individual oysters being found below the low tide level. Farther up Newport River west of Core Creek, oysters are found in planted beds and well-developed oyster reefs, in contrast to their distribution close to the inlet.

Most of these Newport River oyster reefs are long and relatively narrow, and lie at right angles to the main tidal currents (Grave 1901). Whereas loose shells typically comprise the top of a reef, clusters of living oysters grow on both sides and at the ends, cemented to the almost-buried shells of previous generations. These reefs enlarge by attachment and growth of oyster spat on older shells, and by isolated clusters becoming separated from the main reef. Survival and growth are apparently greater at the ends of reefs where stronger currents sweep oysters clean of sediment, supply more oxygen and planktonic food, and carry off excretory wastes. Alongside the reefs, a bottom of shell debris supports a population of scattered oysters, which are harvested by tonging. Oysters on reefs are typically too crowded to have commercial value except as a source of spawn for new generations. Locally these natural reefs are called "oyster rocks," there being no natural occurrence of rock in this area. Besides these natural beds, a number of planted beds are located between Core Creek and Cross Rock.

In high salinity waters of the southeastern states, oysters are typically restricted to the intertidal zone as are those near Beaufort Inlet. Where much lower salinities prevail (i.e., 14 to 20 ‰), small beds of oysters may occur in deep water (Galtsoff & Prytherch 1927). However, the occurrence of subtidal oyster populations in high salinities is rare in the southeastern states (Wells & Gray 1960a). This predominantly intertidal distribution of oysters in high salinity has been attributed to a variety of factors. Galtsoff & Prytherch (1927) and Menzel (1955) have attributed this distribution to the selection of this particular zone by oyster larvae, and their behavior was credited to their stimulation by minute amounts of copper in the uppermost strata of water (Prytherch 1934). However, other workers have blamed various oyster enemies with making life too difficult below low tide for the survival of oysters attaching there. Lunz (1943) concluded that the boring sponge,

Cliona celata, eroded subtidal oyster shells to such a degree that it prevented the development of natural oyster beds in this lower zone. Chestnut & Fahy (1953) suggested that predation of oyster spat by oyster drills, *Urosalpinx cinerea*, offers a partial explanation for this peculiar distribution pattern. Working in North Carolina waters, they found that setting of oysters below low water was much in excess of that above low water and, in general, increased in intensity downward. Predation by *Urosalpinx* diminished in intensity off the bottom; and Mackin (1946) has shown that the higher in the intertidal zone an oyster lies, the less likely it is to be drilled by *Urosalpinx*. Wells & Gray (1960a) have indicated that Gulf oyster drills, *Thais floridana*, probably also contribute to the destruction of subtidal oysters and, therefore, to the restriction of oysters to an intertidal distribution in North Carolina waters. In this respect, other predators of the oyster might be added, particularly those such as starfish which feed on young spat. Together, they could effectively limit oyster survival to the intertidal zone, where periodic exposure affords the oyster some predation.

Previous work on oyster communities of this region has been reported upon by Winslow (1889), Grave (1903), Coker (1907), and Chestnut (1951). They have been primarily concerned with distribution of oyster beds, potential value of areas for commercial management, and their utilization. Grave noted the occurrence of many oyster associates (without naming them) during a period of high salinity on oysters planted near White Rock, and the fact that there were many organisms associated with oyster reefs. Both MacDonald (1940) and the Stephensons (1952) studied vertical zonation of oyster associates, MacDonald in Beaufort Harbor, and the Stephensons on rock jetties and breakwaters near Beaufort Inlet.

PHYSICAL FACTORS

Hydrographic data were collected for Newport River from January 1955 to October 1956 in a series of monthly runs from Shark Shoal to Cross Rock. Although the data from the first two months are somewhat irregular, a systematic procedure adopted in the spring of 1955 produced more satisfactory results. To characterize adequately the salinity gradient of Newport River, it was necessary to collect hydrographic data at the same tidal phase at all stations. A convenient two-hour lag in tidal phase in upper Newport River made this possible. Since minimum salinities were of more interest to the study, being important as a limiting factor to upstream penetration, the runs were scheduled to correspond with low tides.

The nine stations scheduled for each hydrographic run are shown in Fig. 1. Five of these stations (#1, 2, 3, 7, and 9) correspond to the stations chosen for collecting oyster associates. Because bad weather prevented the completion of the March 1956 run, this series is not complete.

TABLE 1. Salinity (‰) of water samples collected in Newport River, N. C., January 1955 to October 1956.

Station	1	2	3	4	5	6	7	8	9
Date	Shark Shoal	Pivers Island	Gallant Point	Newport Marsh	Crab Point	Midway	White Rock	Turtle Rock	Cross Rock
January 31.....	—	32.3	—	—	23.7	—	21.7	—	—
February 26.....	—	—	—	—	24.3	23.0	23.5	20.1	11.1
March 13.....	—	35.5	35.3	34.0	33.2	30.8	30.4	—	28.6
April 17.....	35.9	35.9	32.4	31.8	31.0	30.4	30.1	28.0	23.5
May 7.....	34.8	34.6	32.5	31.4	29.5	29.1	29.1	29.3	29.8
June 28.....	36.6	36.7	36.2	35.3	35.9	35.5	35.3	34.8	35.4
July 19.....	36.3	36.6	36.3	36.0	35.5	34.9	34.6	33.5	29.4
August 2*.....	35.8	35.5	33.3	—	29.8	27.2	26.5	25.0	14.0
August 13.....	21.6	16.5	12.8	9.3	3.9	2.0	4.2	0.8	0.6
August 27*.....	17.7	15.0	11.2	5.6	2.8	5.1	2.1	0.6	0.9
September 11.....	15.3	10.2	7.3	4.2	1.6	2.0	1.7	0.7	0.6
October.....	32.8	31.1	28.1	25.2	23.7	21.8	21.3	21.4	18.7
November 25.....	34.1	32.7	29.9	27.1	28.0	27.5	27.1	25.2	21.4
December 31.....	32.0	30.7	28.2	29.3	25.0	23.5	23.9	21.4	20.4
January 29.....	27.8	25.5	23.0	20.4	18.8	18.2	18.8	15.2	13.9
February 26.....	30.8	27.1	25.5	25.2	21.0	17.9	19.0	13.7	8.4
March 24.....	31.6	30.7	25.1	22.4	—	—	—	—	—
April 28.....	31.5	31.1	24.4	21.8	21.7	19.7	19.2	19.9	12.0
May 29.....	32.0	31.6	27.2	24.3	24.4	22.9	22.4	21.7	20.5
June 21.....	33.5	32.7	28.1	25.8	25.4	25.4	24.8	24.8	19.3
July 20.....	35.0	34.5	32.5	31.0	30.8	29.0	28.8	27.5	11.4
August 18.....	35.8	35.3	35.0	33.2	32.5	32.3	31.9	31.5	27.8
September 3.....	33.1	35.3	34.0	35.7	32.0	31.9	31.4	29.9	24.4
October 6.....	33.1	32.5	29.7	28.0	26.5	26.3	25.8	24.8	22.4
Mean.....	31.77	30.93	28.17	26.57	25.16	24.23	24.05	22.33	18.98
n =	19	21	20	20	21	20	21	19	20

* Stations omitted from mean.

SALINITY

Water samples were sealed in a glass jar in the field, then analyzed in the laboratory with hydrometers following the method recommended by Shureman (1940). Corrections for temperature were applied and density converted to salinity by the use of appropriate tables (Zerbe & Taylor 1953). Salinity data are presented in Table 1.

A salinity gradient is obvious in each month's data except June 1955 when an excessively high salinity prevailed throughout the area studied. This gradient is distinct in the salinity means for each collecting station (Fig. 6). The data for the series of August 2 and August 27, 1955 were excluded from these means, for these series were made between regular monthly runs, and their inclusion would give the low salinity conditions of that period a disproportionate influence on the means.

Salinity is more variable at Cross Rock (#9) than at any other station. It is usually lowest there, as well, because of the influence of the upstream part of Newport River. Typical low-tide salinity profiles show a sharp drop produced by the fresh water flowing by this reef. Occasionally this water extends as far down as Turtle Rock (#8). The broad area of shallow water lying between Turtle Rock and the Intracoastal Waterway channel shows a relatively small gradient in salinity, often with less than 3 ‰ difference at the two extremes.

Several times, however, the salinity at White

Rock (#7) showed a deviation from the expected linear gradient. This was primarily due to water coming from Pamlico Sound via the Clubfoot Canal and entering Newport River through Harlowe Creek. Its effect would be greatest when there is a marked difference in salinity and tide conditions in Pamlico Sound. These factors can operate to increase salinity locally as in the case of January 29 and February 26, or to reduce salinity locally as in the case of April 28, 1956.

Where Core Creek joins Newport River, large amounts of water can flush up and down the dredged channel through Core Creek Canal to Pamlico Sound. This has a direct influence upon water at the nearby station, its salinity being considerably greater than that between stations in the upper part. With decreasing distance from the inlet, the remaining stations possess higher salinities, with the sharpest increase in the vicinity of Gallant Point (#3). Samples collected at the most seaward station, Shark Shoal (#1), often contained water of "ocean salinity" even at low tide. Salinity conditions at the Pivers Island hydrographic station (#2) probably differ very little from those at the nearby Sluiceway collecting station.

The salinity gradient shown by the data seems adequate as a background against which to place the distribution of oyster associates. A possible criticism could be voiced that the gradient does not go low enough, that productive oyster beds (plus associates)

are found in waters of much lower salinity than the 19 ‰ average at Cross Rock, the station with the most brackish conditions. This apparent shortcoming was conveniently corrected by a period of 6-7 weeks of abnormally low salinities which occurred in 1955, providing an opportunity to study distribution in relation to a much lower salinity gradient.

Significant vertical salinity gradients are not found because wind-driven turbulence and strong tidal currents thoroughly mix the water in shallow areas and deeper channels, respectively.

Ordinarily, there is little difference between salinities collected on one low tide and at the following high tide at the same station. On September 13, 1956, less than 1 ‰ difference in salinity was found at consecutive tidal extremes at White Rock or at Pivers Island. However, a difference of as much as 10 ‰ between consecutive tidal extremes was observed immediately after Hurricanes Connie and Diane had produced a steep salinity gradient in the River. Normally, the salinity data obtained yielded a reasonably adequate picture of conditions at the various stations.

During the period of study, the overall salinity level of the waters of Newport River showed broad fluctuations. The records for a single station, White Rock (#7), shown in Fig. 2, are representative. Precipitation at New Bern Airport and air temperatures at Morehead City are shown on the same graph, since they have a controlling influence on salinity in the river. Low rainfall and high air temperatures reduce runoff and river flow and increase evaporation, thus elevating salinity. Such conditions obtained in the period March 13 to July 29, 1955, when salinities in Newport River were very high. In the first ten days of August, a series of inland thunderstorms provided sufficient runoff to restore a normal salinity level. In the next ten days, Hurricanes Connie and Diane produced freshets that radically depressed salinities throughout the length of Newport River; additional heavy rains and a third hurricane (Ione) maintained this altered salinity regime for a period extending well into October. This period of very low salinity was followed by a quick recovery to normal, average salinity conditions resulting from little further rainfall. Average conditions prevailed until the first days of 1956 when a period of low salinities set in which lasted through the first of May. This period of abundant precipitation coupled with low temperatures, produced a typical springtime reduction in estuarine salinity. Salinities increased to average levels in May and June and continued to increase in July as higher temperatures increased evaporation. Generally, salinities remained high for the remainder of the study.

The salinity and temperature data most useful for comparison between years in the Beaufort area are those collected by Gutsell (1930) over a five-year period. Such a comparison shows that low salinities during the spring and high salinities during the summer are not unusual, while the very low salinities re-

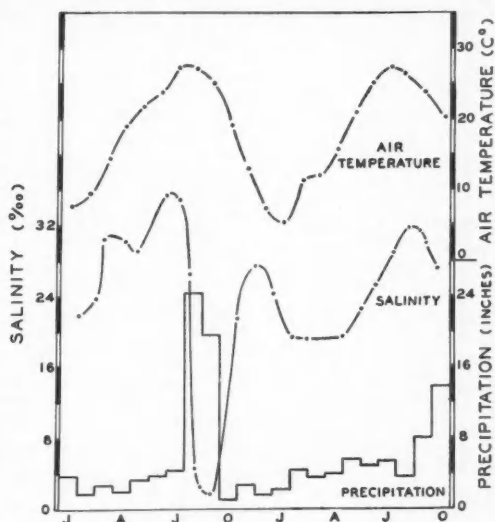


FIG. 2. Relationship of precipitation, air temperature, and salinity in upper Newport River, 1955-1956. Precipitation for New Bern Airport and air temperature for Morehead City (U. S. Weather Bureau 1955, 1956).

corded in August and September 1955, are exceptional. Three of the five years covered by Gutsell's data (1924, 1925, and 1926) showed springtime low salinities equal to or more pronounced than those observed in 1956. Four years (1925, 1926, 1927, and 1928) showed periods of high salinity in mid- or late summer. Only in 1924 was a very low level recorded in September and October similar to the extreme lows of 1955. At that time, a minimum salinity of 6 ‰ was recorded at Pivers Island.

TEMPERATURE

An analysis of the temperature data recorded at each hydrographic station shows that many factors affect them. While the most seaward stations are under the strong conservative influence of the Atlantic Ocean, upriver stations were more responsive to air temperatures. In summer, upriver stations frequently showed temperatures approaching and exceeding 30°C, while in winter these same stations showed water temperatures below 5°C. Generally there was an increasing difference in temperatures between a particular station and the most seaward station, as collecting moved upriver. In winter, the nature of this difference (*i.e.*, whether it was a higher or lower temperature) depended upon the time of day, for upriver stations were colder on mornings and often warmer on afternoons. The average absolute difference from Shark Shoal temperature amounted to 2.24°C at Cross Rock. Thus, the euryhaline organisms which would inhabit upper Newport River must also be able to withstand a wide range of temperature throughout the year and tolerate rapid diurnal changes.

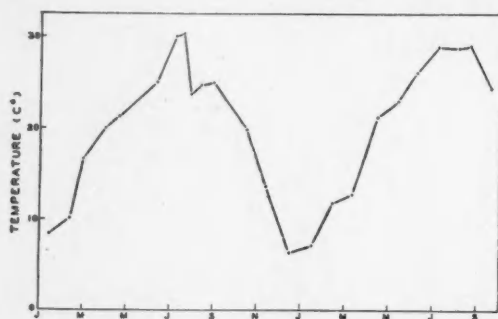


Fig. 3. Water temperature, Pivers Island, 1955-1956.

Because upriver temperatures are so variable and because other workers have recorded comparable temperatures at Pivers Island, the data collected at this location will be used in discussing seasonal trends (Fig. 3).

The period January 1955 to October 1956 exhibited typical thermal maxima between July and September and typical minima in December and January. Two exceptional periods were observed, however: (1) notable reductions in water temperature accompanied the hurricanes; (2) in 1955-56, water temperatures were particularly low in November, December, and January. Generally the spring of 1956 was quite cool, mean air temperatures throughout eastern North Carolina being several degrees lower than average (U.S. Weather Bureau 1956). In consequence of this meteorological deviation, crops were delayed several weeks, and many events depending upon water temperatures were similarly delayed. The oyster set in Pamlico Sound occurred several weeks later than usual (Chestnut, pers. comm.); winter elements continued to dominate the sessile community on rocks and pilings well into July. The arrival of normal summer conditions was considerably delayed.

HYDROGEN ION CONCENTRATION

Hydrogen ion concentrations were determined colorimetrically for most hydrographic collections. Values obtained in February 1956 are shown in Fig. 4 with accompanying salinity and color curves. At this time, salinity values as low as 8.4 ‰ were recorded for upper Newport River. Simultaneously, pH values were also depressed, but only to pH 7.7. Where salinity of river water was above 20 ‰, the hydrogen ion concentration had remained at its normal level for sea water (pH 8.3). Generally, this relationship between pH and salinity values held true, and during periods of high salinity, there were no significant deviations from normal sea water values.

However, during the freshets following the hurricanes, pH values dropped to near-neutral levels, and in a few cases indicated slightly acidic conditions. This situation applied on September 11, 1955, when

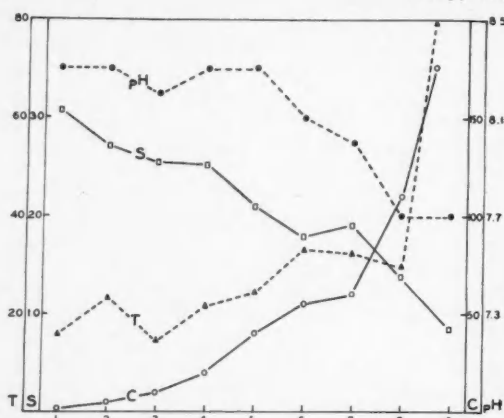


Fig. 4. pH, salinity, and color profiles, February 26, Newport River, 1956. S—salinity in ‰, C—color in ppm, T—turbidity in milligrams of solids per liter of seawater.

salinities in upper Newport River ranged between 2.0 and 0.6 ‰. At three of these stations, pH values were 6.7 (#8), 6.8 (#7), and 6.9 (#6). Meanwhile, the pH of the water collected near Cross Rock (#9) was 7.5. This unusual increase, unaccompanied by a corresponding higher salinity, can be explained as the effect of a buffering action of the reef upon the pH of nearby waters. This hypothesis was later tested in the laboratory where it was found that clean oyster shell would raise the pH of distilled water sufficiently to produce the observed phenomenon. Such conditions undoubtedly help decompose old mollusc shells.

COLOR

For most water samples the amount of color was determined by visual comparison with solutions of known concentration of platinum chloroplatinate. Fig. 4 shows the values for September 11, 1955. In every case, maximum color values were found at Cross Rock and minimum values at Shark Shoal. Distribution of color bears an inverse relationship to salinity. The typical color gradient was obvious in water samples from most runs, and the brownish appearance of water in upper Newport River was equally obvious on most visits.

Probably this brownish color is a product of decay of organic matter farther upstream. Its appearance is that of brownish swamp waters. There, color is attributed to "humic acids" released by decomposing vegetation. With increased rainfall and a greater flow from upstream, an increased amount of color enters the upper part of Newport River to be diluted and eventually precipitated or carried to the ocean. During the period of extremely low salinities following the 1955 hurricanes, color concentrations were high enough at Pivers Island to be obvious to observers.

TURBIDITY

Like color, turbidity was an obvious feature of upper Newport River. Most of the bottom in this part of the river is soft black mud, and wind-driven waves keep it stirred up most of the time. Even at Shark Shoal, however, the water is rarely clear; currents sweeping out of Town Creek, Beaufort Harbor, and Taylor Creek on ebbing tides carry considerable amounts of particulate matter seaward.

Water samples collected on July 20, 1956 were passed through a millipore filter in order to use the particulate matter collected on the cellulose filter disk as a measure of turbidity. With appropriate controls and corrections, these filter disks were dried three hours at 74.5°C and weighed, to obtain the dry weight of the material extracted from the original water samples. The results (Fig. 4) are expressed in terms of milligrams of solids per liter of water, and ranged from 14.6 at Gallant Point (#3) to 80.5 at Cross Rock (#9).

CURRENT

Current measurements were made at each collection station with fluorescein dye, by timing the movement of a marked parcel of water over a measured course. Current velocities were recorded from 10.7 cm/sec to 65.5 cm/sec. Because there was as much variation in current velocity in the immediate vicinity of an oyster bed as there was between beds, this factor did not follow any recognizable pattern between stations.

COLLECTION STATIONS AND METHODS

To present a clear picture of the distribution of oyster associates in relation to the salinity gradient of Newport River, a series of collections were made at five locations. At each collection station there was a sizable natural population of oysters. A description of each station follows; the location of each is indicated in Fig. 5.

1) Shark Shoal—A rock breakwater 500 m long

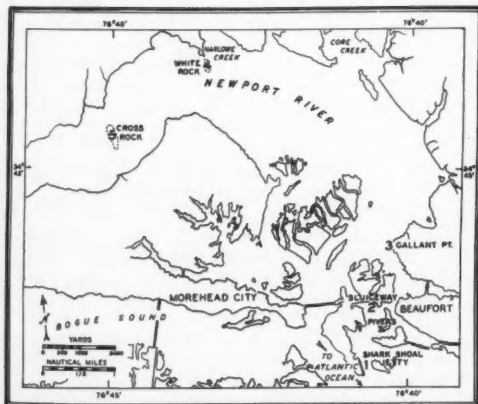


FIG. 5. Chart of Newport River showing the location of collecting stations.

parallels Beaufort Channel and extends southward into deep water. *Crassostrea virginica* is chiefly intertidal, only scattered individuals occurring below low tide. Barnacles and mussels are prominent at higher levels. Behind this breakwater lies a sandy island composed of dredging waste; at places, sand-dwellers can be found among the rocks. The Stephensons (1952) described features of the zonation of plants and animals on this breakwater. Collections were made within 50 m of the southeastern point of the shoal, and extended 0.6 m below the lowest tide.

2) Sluiceway—With each flood-tide, water flows through a narrow entrance to a semi-enclosed lagoon southwest of the intersection of U. S. 70 and Pivers Island Road. At low tide this entrance is about 3 m wide, rock jetties on both sides protecting the sand ridge. Oysters grow in clusters on rocks of these jetties and on rocks and shells on the bottom, extending to a depth of one-half meter below the lowest tides. The overall length of the oyster-covered area is about 45 m. With every tide, strong currents rush in and out through this entrance. At most high tides the area is completely submerged. Hydrographic data collected nearby at Pivers Island would apply to this station with only minor differences.

3) Gallant Point—Extending southward 180 m from Gallant Point itself is a spit or bar of oyster shells that ends in a patch of sand and *Spartina*. This spit is elevated above nearby bottoms as much as 0.8 m. In a semi-enclosed cove behind the bar is a soft mud flat containing large clusters of living oysters. Single oysters and clusters border the outer edge and are found in decreasing numbers toward deep water. These oysters predominated in collections.

4) White Rock—A broad shoal lies immediately west of the point where Harlowe Creek flows into Newport River, which extends 200 m southward into the river. It is composed of oysters and shell and a considerable amount of sand. Although most of the bottom in this part of Newport River is soft mud, there are several natural oyster reefs and several cultivated oyster bottoms nearby. White Rock stands no more than 0.2 m above lower tide levels, but still rises 1 m or more above adjacent bottoms. Most collections were made at high tide by pulling a scallop dredge across the reef with an outboard-powered skiff. The last collection was made at low tide.

5) Cross Rock—This is a typical oyster reef or "rock," 250 m long and up to 10 m wide, a narrow bar of shell elevated less than 1 m above the nearby bottom. It lies astride Newport River with its long axis at right angles to tidal currents. The crest is composed of dead oyster shells, supporting one small patch of *Spartina* with *Modiolus demissus* attached to its roots. Living oysters form the body of the ridge and its sides; clusters and individual oysters are scattered over adjacent mud bottom. These clusters are usually cemented to dead shells imbedded firmly in the mud. Shell fragments are also an important component of the reef. Collections of oysters

and associates were made at low tides, when most of the reef was exposed. In addition to exposed oysters and shell, submerged clusters several meters beyond the low tide mark were often included in collections.

These collection stations were systematically sampled to provide information about the faunal composition of each natural oyster bed. Fifty-four collections made during an 18-month period (from May 1955 to October 1956) are included in this study. Regular monthly collections were made at Shark Shoal, Sluiceway, and Cross Rock, and summer collections only were made at Gallant Point and White Rock. Supplementary collections were made at Sluiceway, White Rock, and Cross Rock in early August 1955, between the regular monthly visits. These extra collections provided a basis for evaluating the effects of the hurricanes which passed through the area in following weeks. (The date and location of each collection are included in Table 3.)

Physical differences between collection stations and the growth habit peculiar to oysters, of attaching to rocks and to one another, made the choice of sampling methods very difficult. The system adopted had to be applicable to intertidal oysters attached to Shark Shoal Jetty as well as those in reef aggregations in the upper part of Newport River. For this reason, a quadrat or area sampling system proved to be impractical. Instead, a volume collecting unit was used—each sample consisting of a gallon of oysters and shell, and the associated organisms. Because the oysters and shell were of the same magnitude of size, the use of a volume collection unit provided comparable samples of the community from both types of natural oyster beds.

At each visit to a collection station, a gallon jar was filled with oysters, their associates and shell. An effort was made to collect from each of the minor variations in the habitat, such as tidal zones, and to have the sample reflect the faunal diversity of the bed. All collections were concerned more with the presence of species, and only secondarily with the relative abundance of individual species.

This collecting procedure permits an analysis of species diversity or number of species in relation to a factor, but only limited confidence can be placed in distribution patterns derived for single species from these data. In any sampling procedure, less abundant species are sporadically represented. The coincidence of their presence with a particular factor may be suggestive of some relationship, but it may be equally due to chance. The chance omission of a species from a particular collection may thus be misleading to a study of distribution of individual species. However, this difficulty may be avoided by consideration of the number of species in each collection, rather than the species themselves. With this approach, the chance omission of a single species has an insignificant effect on the results, and instead, may be counteracted by the inclusion of some other, equally less abundant species. Only for more abun-

dant individual species can sufficient confidence be placed in distribution patterns derived from this collection method.

In the laboratory, collections were preserved in 15-20% neutralized formalin. Later, each collection was sorted, and the species and their relative abundance recorded. For each species separate records were kept of every occurrence in the collections. At least one specimen of each species was placed in a special reference collection. Gaps in the record were due to bad weather and breakage of one jar.

Because the coverage of fish was incomplete, rotenone poisoning was used at Gallant Point in September 1956 to collect representatives of the many small fish that frequent shell bottoms. Although several species were added to the list from these collections, the coverage of fish remains inadequate, for their collection requires different collecting techniques.

FAUNAL COMPOSITION

The 303 species collected are listed in Table 2. This total includes 2 protozoans, 12 sponges, 14 coelenterates, 8 flatworms, 4 nemerteans, 99 molluscs, 42 annelids, 2 sipunculids, 76 arthropods, 20 bryozoans, 5 echinoderms, and 19 chordates. No attempt was made to identify other protozoans, or any copepods, ostracods, or nematodes. The protozoans listed were obvious because of their large size or prominence *en masse*. Man and the herring gull could be added to this list, for each has been observed foraging for clams among oysters and shell. Grateful acknowledgement is made to Dr. F. M. Bayer of the United States National Museum for the identification of gorgonians, to Dr. J. P. E. Morrison and Dr. H. A. Rehder of the United States National Museum for the identification of several molluscs, to Dr. Ernst Marcus of the University of Sao Paulo for the identification of nudibranchs, to Dr. Lyman Toulman of Florida State University for the identification of *Poreoponides*, and to Dr. F. J. S. Maturo of the University of Florida for the identification of several bryozoans.

TABLE 2. List of species collected on oyster beds, Newport River, N. C., 1955-1956.

Protozoa:

Folliculinid

Poreoponides cf. lateralis (Terquem).

Porifera:

Cliona celata Grant; *Cliona lobata* Hancock; *Cliona spirilla* Old; *Cliona truitti* Old; *Cliona vastifica* Hancock; *Dictyoclonia adioristica* de Laubenfels; *Haliclona permollis* (Bowerbank); *Halisarca* sp.; *Hymeniacion heliophila* (Parker); *Lissodendoryx isodictyalis* (Carter); *Microcliona prolifera* (Ellis & Solander); *Scypha barbadensis* (Schuffner).

Coelenterata:

Aiptasia eruptaurantia (Field); *Aiptasia pallida* (Verrill); *Astrangia astraeiformis* Milne-Edwards & Haime; *Bunodosoma cavernata* (Andrews); *Diadumene leucolela* (Verrill); *Diadumene luciae* (Verrill); *Epizoanthus americanus* Verrill; *Eudendrium carneum* Clarke; *Hy-*

dractinia echinata (Fleming); *Leptogorgia setacea* (Pallas); *Leptogorgia virgulata* (Lamarek); *Obelia* sp.; *Oculina arbuscula* Verrill; *Tabularia crocea* (Agassiz).

Platyhelminthes:

Bdelloura candida (Girard); *Euplana gracilis* (Girard); *Gnecioceros floridana* (Pearse); *Latocestus whartoni* (Pearse); *Oligocladus floridanus* Pearse; *Prosthlostomum lobatum* Pearse; *Stylochus ellipticus* (Girard); Turbellarian.

Nemertea:

Amphiporus ochraceus (Verrill); *Micrura leidy* (Verrill); *Tetrastemma elegans* (Girard); *Tabulanus pelucidus* (Coe).

Mollusca: Amphineura:

Chaetopleura apiculata Say.

Gastropoda: Prosobranchia:

Anachis avara avara Say; *Anachis floridana* Rehder; *Anachis translirata* Ravenel; *Bittium varium* Pfeiffer; *Busycon canaliculatum* (Linne); *Busycon carica* (Gmelin); *Busycon contrarium* Conrad; *Cacum pulchellum* Stimpson; *Calliostoma euglyptum* A. Adams; *Cantharus tinctus* Conrad; *Cerithiopsis greeni* C. B. Adams; *Cerithiopsis subulata* Montagu; *Cerithium floridanum* Moreh; *Crepidula conveza* Say; *Crepidula fornicata* Say; *Crepidula plana* Say; *Diodora cayenensis* Lamarek; *Epitonium apiculatum* (Dall); *Epitonium humphreysi* Kiener; *Eupleura caudata* Say; *Fasciolaria hunteria* (Perry); *Hydrobia minuta* Totten; *Littorina irrorata* (Say); *Mangelia guarani* Orbigny; *Mangelia plicosa* C. B. Adams; *Melanella conoidea* Kurtz & Stimpson; *Mitrella lunata* Say; *Murex fulvescens* Sowerby; *Nassarius obsoletus* (Say); *Nassarius vibex* (Say); *Neosimnia uniplicata* (Sowerby); *Niso interrupta* Sowerby; *Pleuroploca gigantea* (Kiener); *Rissoina chesneli* Michaud; *Rissoina decussata* Montagu; *Seila adamsi* H. C. Lea; *Thais floridana* Conrad; *Triphora nigrocincta* C. B. Adams; *Urosalpinx cinerea* Say.

Opisthobranchia:

Ancula evelinae Marcus; *Aplysia morio* Verrill; *Berghia coerulescens* (Laurillard); *Catrina tina* Marcus; *Chromodoris aila* Marcus; *Corambella baratariae* Harry; *Cratena kaoruae* Marcus; *Dondice occidentalis* (Engel); *Doriopsilla leia* Marcus; *Doriopsilla pharpa* Marcus; *Hermaca dendritica* Alder & Hancock; *Miesca evelinae* (Marcus); *Odostomia dianthophila* Wells & Wells; *Odostomia dur* Dall & Bartsch; *Odostomia impressa* Say; *Odostomia modesta* Stimpson; *Odostomia seminuda* C. B. Adams; *Okenia impeza* Marcus; *Polycera hummi* Abbott; *Tritonia wellsi* Marcus; *Turbonilla interrupta* Totten.

Pelecypoda:

Abra aequalis Say; *Aequipecten irradians concentricus* (Say); *Anadara ovalis* Bruguiere; *Anomia simplex* Orbigny; *Arca umbonata* Lamarek; *Arcopsis adamsi* Smith; *Atrina rigida* (Solander); *Barbatia candida* Helbling; *Brachidontes exustus* (Linne); *Brachidontes recurvus* Rafinesque; *Chama macrophylla* Gmelin; *Chione cancellata* (Linne); *Chione grus* Holmes; *Congeria leucophaeata* Conrad; *Corbula swiftiana* C. B. Adams; *Crassostrea virginica* (Gmelin); *Cumingia tellinoides* Conrad; *Diplodonta punctata* Say; *Diplodonta semiaspera* Philippi; *Gemma gemma purpurea* Lea; *Hiatella striata* (Fleuriau); *Lima pellucida* C. B. Adams; *Lithophaga bisulcata* Orbigny; *Lyonsia hyalina* Conrad; *Martesia smithi* Tryon; *Mercenaria mercenaria* (Linne);

Modiolus americanus Leach; *Modiolus demissus* Dillwyn; *Mulinia lateralis* Say; *Musculus lateralis* Say; *Mytilus edulis* Linne; *Noetia ponderosa* (Say); *Ostrea equestris* Born; *Petricola pholidiformis* Lamarek; *Pteria colymbus* Roding; *Rangia cuneata* Gray; *Roccellaria hians* Gmelin; *Rupellaria typica* (Jonas); *Tagelus plebius* Solander.

Annelida: Oligochaeta:

Enchytraeus albidus Henle.

Polychaeta:

Amphitrite ornata (Leidy); *Armandia agilis* (Andrews); *Autolytus varians* Verrill; *Aziothella mucosa* (Andrews); *Capitella capitata* (Fabricius); *Cistenides gouldii* Verrill; *Dexiospira spirillum* (Linne); *Diopatra cuprea* (Bosc); *Dorvillea sociabilis* (Webster); *Eteone heteropoda* Hartman; *Eumida sanguinea* (Oersted); *Eunice rubra* Grube; *Eupomatus dianthus* (Verrill); *Glycera americana* Leidy; *Haplosyllis spongicola* (Grube); *Harmothoe aculeata* Andrews; *Heteromastus filiformis* (Claparede); *Hypsicomus torquatus* (Grube); *Lepidametria commensalis* Webster; *Lepidonotus sublevis* Verrill; *Lepidonotus variabilis* Webster; *Loimia medusa* (Savigny); *Marphysa sanguinea* (Montagu); *Naineris laevigata* (Grube); *Neanthes succinea* (Frey & Leuckart); *Nereiphylla fragilis* (Webster); *Nereis occidentalis* Hartman; *Petaloproctus socialis* Andrews; *Pista palmata* (Verrill); *Podarke nr. guanica* Hoagland; *Polydora websteri* Hartman; *Prionospio treadwelli* Hartman; *Pseudopotamilla reniformis* (Muller); *Sabella melanostigma* Schmarda; *Sabella microphthalma* Verrill; *Sabellaria vulgaris* Verrill; *Spiofanus bombyx* (Claparede); *Streblospio benedicti* Webster; *Terebella rubra* (Verrill); *Tharyx setigera* Hartman; *Thelepus setosus* (Quatrefages).

Sipunculida:

Aspidosiphon parvulus Gerould; *Physcosoma capitatum* Gerould.

Arthropoda: Amphipoda:

Caprella acutifrons Latreille; *Caprella linearis* (Linne); *Carinogammarus mucronatus* (Linne); *Corophium cylindricum* (Say); *Gammarus locusta* (Linne); *Jassa marmorata* Holmes; *Melita appendiculata* (Say); *Melita dentata* (Krøyer).

Isopoda:

Cassidiscus lunifrons (Richardson); *Chiridotea caeca* (Say); *Cilicaca caudata* (Say); *Cyathura carinata* (Krøyer); *Dynamene perforata* Moore; *Erichsonella filiformis* (Say); *Idothea baltica* (Pallas); *Leptochelia rapax* Harger; *Leptochelia savignyi* (Krøyer); *Ligia exotica* Roux; *Limnoria lignorum* (Rathke); *Sphaeroma quadridentata* Say.

Decapoda:

Alpheus armillatus Milne-Edwards; *Alpheus heterochaelis* Say; *Alpheus packardii* Kingsley; *Callinectes ornatus* Orbigny; *Callinectes sapidus* Rathbun; *Cancer irroratus* Say; *Clibanarius vittatus* (Bosc); *Eurypanopeus depressus* (Smith); *Heterocrypta granulata* (Gibbes); *Hexapanopeus angustifrons* (Benedict & Rathbun); *Hippolytina wurdemanni* (Gibbes); *Hippolyte pleurocantha* (Stimpson); *Libinia dubia* Milne-Edwards; *Libinia emarginata* Leach; *Menippe mercenaria* (Say); *Metoporphaphis calcarata* (Say); *Neopanope texana* sayi (Smith); *Neopanope* sp.; *Neopontonides beaufortensis* Borradaile; *Pachygrapsus transversus* Gibbes; *Pagurus*

longicarpus Say; *Pagurus pollicaris* Say; *Palaemonetes intermedius* Holthuis; *Palaemonetes pugio* Holthuis; *Palaemonetes vulgaris* (Say); *Panopeus herbsti* Milne-Edwards; *Pelia mutica* (Gibbes); *Penaeus aztecus* (Ives); *Petrolisthes galathinus* (Bosc); *Pilumnus dasyopodus* Kingsley; *Pilumnus lacteus* Stimpson; *Pilumnus sayi* Rathbun; *Pinniza cylindrica* (Say); *Pinnotheres ostreum* Say; *Plagusia depressa* (Fabricius); *Porcellana soriatia* Say; *Portunus* sp. juv.; *Rithropanopeus harrisi* (Gould); *Sesarma cinerea* Say; *Sicyonia laevigata* Stimpson; *Synalpheus townsendi* Coutiere; *Thor floridanus* Kingsley; *Uca pugnator* (Bosc).

Cirripedia:

Alcippe lampas Hancock; *Balanus amphitrite niveus* Darwin; *Balanus eburneus* Gould; *Balanus improvisus* Darwin; *Balanus tintinnabulum* Linne; *Chthamalus fragilis* Darwin.

Insecta:

Anurida maritima (Guerin); Dipteran larva, green; Dipteran larva, yellow.

Pycnogonida:

Anoplodactylus lentus Wilson; *Nymphon rubrum* Hodge; *Tanystylum orbiculare* Wilson.

Xiphosurida:

Limulus polyphemus Linne.

Bryozoa—Entoprocta:

Pedicellina cernua (Pallas).

Bryozoa—Ectoprocta:

Aeverillia setigera (Hincks); *Alcyonidium hauflii* Marcus; *Alcyonidium polyomm* (Hassall); *Amathia convoluta* Lomouroux; *Amathia distans* Busk; *Anguinella palmata* van Beneden; *Bowerbankia gracilis* Leidy; *Bugula californica* Robertson; *Bugula neritina* (Linne); *Cryptosula pallasiana* (Moll); *Electra crustulenta* (Pallas); *Electra hastingsae* Marcus; *Membranipora tenuis* Desor; *Microperella ciliata* (Pallas); *Nolella stipata* Gosse; *Parasmittina trispinosa* (Johnston); *Schizoporella cornuta* (Gabb & Horn); *Schizoporella unicornis* (Johnston); *Victorella pavidia* Kent.

Echinodermata:

Arbacia punctulata (Lamarck); *Asterias forbesi* (Desor); *Lytechinus variegatus* (Lamarck); *Ophiothrix angulata* (Say); *Thyone briareus* (Lesueur).

Chordata: Urochordata:

Ascidia interrupta (Traustedt); *Didemnum litarium* Van Name; *Molgula manhattensis* DeKay; *Perophora viridis* Verrill; *Styela plicata* (Lesueur).

Vertebrata:

Ancylosetta quadrocellata Gill; *Chaetodipterus faber* (Broussonet); *Chasmodes bosquianus* (Lacepede); *Fundulus majalis* (Walbaum); *Gobiosox virgatus* Jordan & Gilbert; *Gobionellus boleosoma* (Jordan & Gilbert); *Gobiosoma bosci* (Lacepede); *Hippocampus hudsonius* DeKay; *Hypleurochilus geminatus* (Wood); *Hypsoblennius hentz* (Lesueur); *Opsanus tau* (Linne); *Orthopristis chrysopterus* (Linne); *Paralichthys dentatus* (Linne); *Synodus foetens* (Linne).

This list (Table 2) contains the macroscopic species identified from 18 months' collecting in the oyster bed community. In addition to typical inhabitants of oyster beds, it includes several influents

from other habitats: *Diopatra cuprea*, *Cistenides gouldii*, and *Nassarius vibex* from nearby sand flats, *Nassarius obsoletus* from nearby mud, and *Uca pugnator* and *Littorina irrorata* from sandy *Spartina* beds.

Of species typically associated with oysters and shell, most are encrusting organisms which find attachment on shells: protozoans, most sponges, coelenterates, bryozoans, barnacles, ascidians, *Eupomatus dianthus*, *Sabellaria vulgaris*, *Sabella* spp., *Anomia simplex*, *Chama macerophylla*, *Ostrea equestris*, *Crassostrea virginica*, *Crepidula* spp., *Diodora cayoensis*, *Brachidontes* spp., *Mytilus edulis*, *Modiolus* spp., *Musculus lateralis*, *Arca umbonata*, *Arcopsis adamsi*, *Barbatia candida*, *Congeria leucophaea*, and *Pteria colymbus*.

A number of the remaining animals live among these sessile forms, usually depending on them or on algae for food: many annelids, many decapods, amphipods, isopods, insects, pycnogonids, nemerteans, flatworms, echinoderms, some fish, many gastropods, sipunculids, and *Chaetopleura apiculata*. In crevices between shells may be found many of the above animals, plus those which find shelter a primary reason for their presence in the oyster bed: *Chione grus*, *Musculus lateralis*, *Petricola pholadiformis*, *Rupellaria typica*, *Lima pellucida*, *Hiatella striata*, *Petrolisthes galathinus*, *Eurypanopeus depressus*, shrimp, isopods, *Nereiphylla fragilis*, and *Thyone briareus*.

The following animals actively burrow into oyster shells: *Cliona* spp., *Lithophaga bisulcata*, *Martesia smithi*, *Roccellaria hians*, *Polydora websteri*, and *Alcippe lampas*. *Hypsicomus torquatus* is found in burrows in shell made by these organisms. Active predators of oysters and other molluscs include *Urosalpinx cinerea*, *Fasciolaria hunteria*, *Thais floridana*, *Pleuroploca gigantea*, *Murex fulvescens*, *Eupleura caudata*, *Asterias forbesi*, *Callinectes* spp., many other decapods, some fish, and *Stylochus ellipticus*. To this list of oyster pests should be added the oyster crab *Pinnotheres ostreum*, which steals its food from the oyster's gills (Stauber 1945, Christensen & McDermott 1958), and the pyramidellid snail *Odostomia impressa*, which lives as an ectoparasite of the oyster, feeding on body fluids or tissue debris from the oyster's mantle (Hopkins 1956b).

In the substrate between oysters, or under them are found *Amphitrite ornata*, many annelids, decapods, *Limulus polyphemus*, *Mercenaria mercenaria*, *Chione cancellata*, *Rangia cuneata*, *Mulinia lateralis*, *Tagelus plebius*, *Lyonsia hyalina*, *Aequipecten irradians concentricus*, *Anadara ovalis*, *Atrina rigida*, and *Corbula swiftiana*.

Many arthropods and annelids, and several gastropods serve as scavengers in the community.

In his classic study of an *Ostrea edulis* oyster bed in the North Sea, Möbius (1877) described oyster beds as being richer in all kinds of animal life than any other portion of the seabottom. He listed 24 species of animals. Later, Caspers (1950) enumerated a total of 208 species that had been collected

on this same North Sea bed. Mistakidis (1951) listed 92 and 116 species in two beds of *Ostrea edulis* in England. Korringa (1951), working on animals inhabiting the shell of *Ostrea edulis*, arrived at a total of 136 species in the epifauna, of which 38 were annelids. This total included 27 copepods, 6 ostracods, and 17 nematodes, groups not covered in the present study.

In studying beds of *Ostrea sinuata*, Fleming (1952) listed 101 species dredged in Australian waters. Mattox (1949) referred to 37 species occurring with *Crassostrea rhizophorae* in Puerto Rico.

The only available detailed surveys of organisms associated with *Crassostrea virginica* are those of Frey (1946) for Potomac River beds, and of Pearse & Wharton (1938) for Apalachicola Bay beds. Frey's list includes only 53 species. This relatively low number of species undoubtedly reflects the lower salinity of the area studied. In contrast, 139 species were listed by Pearse & Wharton. Puffer & Emerson (1953) listed 11 molluscs from oyster reefs in Texas.

of which nine species are included in the present list, with ecological equivalents of the remaining forms. From oysters in Beaufort Harbor, MacDonald (1940) listed 68 species, and the Stephenson (1952) found 105 species (both plant and animal) common on Beaufort jetties and breakwaters. Most of the animals these authors mention have been collected with oysters at Shark Shoal in this study.

It is clear that the oyster bed can support a large fauna. The 303 species collected in the present study exceed the numbers found in other areas with *Crassostrea virginica* or with other oyster species. Nevertheless, the resemblance of these lists is notable; many genera are equally represented on widely separated beds in association with different species of oyster.

DISTRIBUTION

Records of the occurrence of each species were analyzed for trends that might be related to progression of the seasons, to salt content of the water, or to effects of hurricanes. For these analyses, re-

TABLE 3. Occurrence of species present in more than 40% of collections.

Species	SHARK SHOAL							SLUCEWAY							GALLANT Pt.		WHITE ROCK		CROSS ROCK															
	7/20/55	8/31/55	9/12/55	10/25/55	11/25/55	12/25/55	1/25/56	7/20/55	8/31/55	9/12/55	10/25/55	11/25/55	12/25/55	1/25/56	7/20/55	8/31/55	9/12/55	10/25/55	11/25/55	12/25/55	1/25/56	7/20/55	8/31/55	9/12/55	10/25/55	11/25/55	12/25/55	1/25/56	7/20/55	8/31/55	9/12/55	10/25/55	11/25/55	12/25/55
<i>Neanthes succinea</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Nereis occidentalis</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Melita dentata</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Balanus imprints</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Eurypanopeus depressus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Polydora websteri</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Corophium cylindricum</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Polliculinid</i> species	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Eupomatus dianthus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Balanus eburneus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Sabellaria vulgaris</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Aiphasia pallida</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>A. erythrauranta</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Diadumene luciae</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>D. leucolena</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Brachidontes exustus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Nereiphylla fragilis</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Odotomia impressa</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Electra crustulenta</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Obelia</i> species	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Sabella microphthalma</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Mitrella lunata</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Capitella capitata</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Odotomia dianthophila</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Otrea equestris</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Schizoporella unicornis</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Amphiporus ochraceus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Bugula neritina</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Membranipora tenuis</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Cliona celata</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Urosalpinx cinerea</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Marphysa sanguinea</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Gammarus locusta</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Lithophaga biuclata</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Molgula manhattensis</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Haplosyllis spongicola</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Balanus amphitrite</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Melita appendiculata</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Pinnotheres ostreum</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Caprella acutifrons</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x

With the reproductive periods determined by McDougall as a guide, the animals collected in this study have been segregated into three categories on the basis of their seasonal occurrence: winter species, summer species, or species present throughout the year. The great majority fit the year-round category,

although low salinity may have curtailed the distribution of certain species at times. These 200 species constitute the basic structure of the oyster bed community. Winter and summer components appear, flourish to varying degrees, and disappear in their season, representing but a fraction of the species found in the beds.

Winter species comprise a distinct unit (Table 5), a temporal sub-community within the oyster bed, whose appearance on a bed is relatively noticeable. The most obvious feature is the presence of *Tubularia crocea*, a colonial hydroid which is the basic element of this winter component. Probably many other species depend on it for food or attachment. Hundreds of the elongate amphipod, *Caprella linearis*, cling to its stalks and feed on the polyps. A second amphipod, *Jassa marmorata*, likely depends on *Tubularia* for food, and several nudibranchs presumably feed upon its polyps also. One species, *Hermæa dendritica*, was very numerous in March 1956, when 41 specimens were recovered in a gallon-jar sample of oysters and shell. Another important member of the winter faunal component, the edible mussel *Mytilus edulis*, may require the presence of such hydroid colonies for attachment of its spat (Korringa 1951). The bryozoan *Aeverillia setigera* also usually attaches to hydroid stems.

While *Tubularia* protoplasm may survive the warm season at Beaufort in a dormant state within old hydrocauli as reported by McDougall, it seems unlikely that all eleven species in this winter group similarly remain secreted in the area. The case of *Mytilus edulis* is outstanding. Adults of that species cannot endure the high temperatures of summer in this area, and individuals which appear one winter disappear the following summer before attaining any appreciable size (Wells & Gray 1960b). This recurrent winter population owes its presence to planktonic larvae brought into the estuary by tidal currents. Most likely these *Mytilus* larvae and those of most species in this winter group have been carried southward by storm-induced water currents from population centers north of Cape Hatteras. Bumpus & Pierce (1955) have suggested that such a water movement is responsible for the winter-spring occurrence of the anomalous species of northern affinities found by Williams (1948, 1949) and Suitcliffe (1950) in the northern part of the Carolinian subprovince.

The summer species (Table 5) do not show the cohesiveness of the winter group. *Eudendrium* and the colonial ascidian *Perophora* may survive the unfavorable seasons as dormant protoplasm in small bits of stolon and hydrorhiza. Several species may owe their occurrence to planktonic larvae brought northward in ocean currents. A group of nine decapods has been included among this summer component of the fauna of oyster beds. They were present only in collections made during the warmer months. Probably these do not leave the area, but overwinter in a dormant state in deep water or buried

TABLE 5. Seasonal composition of oyster bed fauna, Newport River, May 1955 to October 1956.

Species	Dates of Collection
Winter	
<i>Tubularia crocea</i>	10/56-6/56
<i>Caprella linearis</i>	10/55-7/56
<i>Jassa marmorata</i>	10/55-5/56
<i>Hermæa dendritica</i>	10/55-3/56
<i>Berghia coerulescens</i>	5/56
<i>Cratena kaoruae</i>	3/56-6/56
<i>Corambella baratariae</i>	1/56-7/56
<i>Aeverillia setigera</i>	11/55-4/56
<i>Mytilus edulis</i>	1/56-7/56
<i>Cancer irroratus</i>	4/56
<i>Balanus tintinnabulum</i>	11/55-3/56
Summer	
<i>Eudendrium carneum</i>	7- 9/55
<i>Perophora viridis</i>	7- 8/55, 7- 8/56
<i>Tanystylum orbiculare</i>	7- 9/55, 7-10/56
<i>Amathia distans</i>	7- 8/55, 5- 9/56
<i>Catriona tina</i>	8-10/55, 8/56
<i>Dictyociona adriatica</i>	7/56
<i>Chaetodipterus faber</i>	8/56
<i>Harmothoe aculeata</i>	7/55, 7/56
<i>Amathia convoluta</i>	8/56
<i>Abra aequalis</i>	7/55, 6- 9/56
Decapods:	
<i>Pelidnota mutica</i>	6- 7/55, 7- 9/56
<i>Rithropanopeus harrisi</i>	6-10/55, 6- 9/56
<i>Hexapanopeus angustifrons</i>	7-10/55, 5- 7/56
<i>Pagurus longicarpus</i>	7-11/55, 8-10/56
<i>Hippolyte pleuracantha</i>	7/55, 9-10/56
<i>Callinectes sapidus</i>	6-10/55, 5- 9/56
<i>Callinectes ornatus</i>	7-10/55, 7/56
<i>Pinnixa cylindrica</i>	7/55, 7/56
<i>Sesarma cinerea</i>	8/55

in the bottom. The blue crab *Callinectes sapidus* exhibits such behavior in Chesapeake Bay (Churchill 1919). In contrast to other decapod species that were found in an active state in winter, these species effectively withdrew from the oyster bed community.

Sixty-five species could not be classified on the basis of their seasonal occurrence because the data were insufficient.

As has been noted in the discussion of water temperatures, the spring of 1956 was late, and extended into the "summer months." Consequently, winter forms remained in this area until mid-July, although *Tubularia* colonies normally begin to slough off in early June. Abnormally low temperatures allowed the prolonged occupation of this area by winter forms. In the preceding fall, low salinities had prepared shell surfaces, and led to an early occupation by these winter forms. With an early start and a late demise, the 1955-56 winter fauna stayed an unusually long time.

NUMBER OF SPECIES

Many workers have made surveys of the distribution of a single species or of a taxonomic group in relation to salinity (e.g., McDermott & Flower 1953,

Hopkins 1956a). Their concern with particular species is largely due to economic considerations. Some are utilized by man for food, while others are predators or pests associated with economically important species. A number of broad studies have been conducted on distribution of many phyla in relation to salinity (Gunter 1950, Batchelder 1926, Filice 1954, Ferroniere 1901, Hoese 1960, Parker 1956, 1959, Pearse 1936, Percival 1929). Many of these studies do not make a distinct separation of the effects of salinity from those of substrate; they include organisms from a wide variety of bottom types. However, mud bottoms may support a richer fauna than sand bottoms, and rock bottoms may support a richer fauna than mud bottoms (Filice 1954, 1958). Moreover, the distribution of these bottom types may be directly related to their distance from the open ocean. In combination, these conditions can seriously obscure the effects of salinity on the distribution of organisms, for the affinity of many species for a particular bottom type would limit their distribution to that substrate, and would not show their potential distribution in relation to salinity. In contrast, all collections in the present study were made on the same type of substrate—oysters and shell. Only minor effects are produced by the inclusion of strays from nearby habitats.

The number of species recorded from each collection can be used as a measure of the severity of environmental conditions. For each station, the mean number of species per collection has been computed and compared with the mean salinity for each station (Fig. 6). The average gallon-jar sample

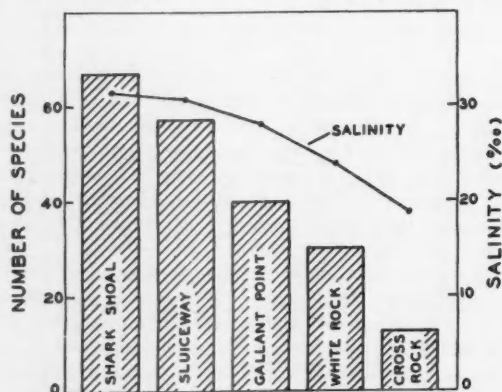


FIG. 6. Mean number of species collected and mean salinity for each station.

would have contained 43 species of oyster associates.

The number of species falls off dramatically in fresher waters. The mean number decreases in a regular fashion from the river mouth to the most upstream station. The total number collected at each station is included in Table 6. This statistic also shows the presence of many more species near the ocean, with decreasing numbers the farther upstream the station is situated.

In an attempt to characterize further the five stations on the basis of species distribution, each species was assigned a "normal salinity limit," beyond which a species penetrates only at times of very high salinity. The number of species that find their normal limit at each station has also been entered in Table 6. Although many of the 51 species found at Cross Rock probably extend farther upstream, the 114 species found at Sluiceway normally do not reach Gallant Point, the next station upstream. Presumably, salinity or some other condition stops more species in this relatively short distance than in any comparable length of the river. The least important gap lies between White Rock and Cross Rock, for only 33 of the species that reach White Rock do not also reach Cross Rock; this may be attributed to the general similarity of salinity conditions in that part of upper Newport River. The apparent sharpness of the break above Sluiceway and the reduction in species above White Rock may derive in part from the greater number of collections at Sluiceway and Cross Rock as contrasted with the two intervening stations. However, different parts of the salinity gradient are not equally effective in halting the upstream penetration of species. In recognition of the critical nature of that part of the salinity gradient, Redeke (1922) placed the division between "sea water" and "brackish water" at 30 ‰ salinity. Under normal conditions the 30 ‰ isohaline is located between Sluiceway and Gallant Point, and corresponds to the marked reduction in species upstream from this position. Although collecting intensity may be a contributing factor, hydrographic data support the second interpretation.

Apparent differences in the basic data represented in the second and third lines in Table 6 are due to the exclusion of several species from upstream station lists when they occurred there only once or twice at times of very high salinity, and to the occurrence at upstream stations of more than 70 species that were not collected at more seaward stations. Most of those species from upstream stations were collected only infrequently; only one species was characteristic of upstream stations and not found downstream. This animal, the isopod *Cassidiscia lunifrons*, was usually found by the hundreds among oysters at Cross Rock, and was less abundant at White Rock, and absent from those stations below White Rock. Although found in numbers upstream, other so-called typical brackish forms were also collected at stations close to the ocean. This was true of the mussel *Brachidontes recurvus* and the bryozoans *Electra crustulenta* and *Victorella pavidia*.

One fault inherent in the collection method used is the possibility that particular species may be omitted from certain collections by chance or because of conditions causing that species to be more secretive, or unfavorable tidal or weather conditions limiting the thoroughness of the collector. For this reason, a species-centered approach has been avoided in this study, and instead, the analysis of distribution

TABLE 6. Number of species collected in relation to salinity.

	Shark Shoal	Sluiceway	Gallant Point	White Rock	Cross Rock	Total
Mean number of species.....	67.0	57.6	40.1	30.0	16.3	43.4
Total number of species.....	220	203	105	92	56	303
Number of spp. with upstream limit there.....	50	114	42	33	51	—
Mean salinity (o/oo)...	31.8	30.9	28.2	24.0	19.0	—

deals primarily with the numbers of species in each collection. The omission of one species from a particular collection may be offset by the omission of another at the next collection, and with 300 species to consider, fluctuations of this magnitude do not assume the importance they might in a species-centered study.

In Table 6, the mean and total numbers of species have been used as measures of species diversity at each station, which is directly related to the salinity regime.

At Shark Shoal, many mussels and barnacles live between and upon the oysters, and many algae, sea anemones, hydroids, bryozoans, and sessile annelids attach to them. *Ostrea equestris* is abundant. Many crabs, annelids, and snails scramble and crawl through the growths, and starfish and *Arbacia* cling to oyster clusters and the rocks to which they are attached. Blennies hide in the crevices. The jetty is rich with species.

Typically at Sluiceway, sponges are more obvious, echinoderms are rarer, and clams are found on the bottom between oyster clumps. Otherwise, the general appearance of this bed is biologically similar to Shark Shoal, with bryozoans and algae prominent.

Gallant Point is inhabited by a smaller group of animals among which the oyster drill *Urosalpinx* is prominent. Almost every phylum is sparingly represented, with only certain species of decapods and molluscs in abundance. Algae are still well represented, but no sponges are evident.

White Rock harbors the species typically found at Cross Rock with several additions, including *Nassarius vibex*, *Pagurus longicarpus*, many *Crepidula*, and fish caught by dredging. The number of species for White Rock is boosted by the incursion of *Ostrea*, *Leptogorgia*, and several other high salinity forms at times of high salinity.

At Cross Rock, fewer species were present, but they were often represented by large numbers of organisms. Sessile foliicolinid protozoans, hydroids, barnacles, and bryozoans *Electra crustulenta* and *Victorella pavida* encrust the shells and hold sediments deposited by the river. Amphipods are usually numerous, *Corophium* building mud tubes upon the shells and further adding to the accumulation of sediment. In crevices between oysters are several

xanthid crabs, *Odostomia impressa*, hooked mussels (*Brachidontes recurvus*), isopods, gobies, and several annelids. The annelids present are chiefly those which can burrow into the substrate or hide in these crevices between shells: *Streblospio*, *Nereis*, *Neanthes*, and *Polydora*. Algae were numerous only during a high salinity period.

EFFECT OF HURRICANES

Eastern North Carolina has a long history of the visitations of severe tropical storms and hurricanes. In 1954, hurricanes Carol, Edna, and Hazel affected the region; in 1955, Connie, Diane, and Ione; and in 1956, Flossy. The passage of three hurricanes during the progress of this study afforded an opportunity to observe the effects of such tropical storms on oyster beds of this region. In view of the frequency of tropical storms of such intensity on this coast, their effects must be included as a characteristic part of the environment.

The summer of 1955 was marked by several abnormal weather features which culminated in an unusually early and active hurricane season (Namiias & Dunn 1955). The "jet stream" was located much farther north than usual, permitting hurricanes to move farther over the mainland before being carried out to sea (Kutschenreuter 1956). Abnormally high coastal sea-surface temperatures and southeasterly winds combined to bring an abundance of moisture-laden air over the eastern seaboard. Acting together, these factors created favorable conditions for the movement of hurricanes through eastern North Carolina, and the production of abnormally large amounts of precipitation (Kutschenreuter 1956).

Hurricane Connie crossed the United States coastline in the Beaufort area on August 12; hurricane Diane came ashore near Wilmington, N. C., on August 17; and hurricane Ione passed through this area on September 19.

While hurricanes may have many other effects upon land communities (Visser 1925), the principal effect of these 1955 storms on oyster beds of Newport River was a radical change in salinity. Each storm brought excessive precipitation to the area, profoundly affecting oysters and their associates. One estimate of damage to the oyster industry of the middle Atlantic states by these hurricanes was placed at \$10,000,000 (Dunn 1956). Whereas rainfall in the first six months of 1955 had been little more than 3 inches per month, August and September had 22 and 21 inches, respectively. Hurricane Connie deposited 13 inches of rainfall on the area; Diane, 7 inches less than a week later; and Ione deposited another 13 inches a month later. The large amount of fresh water that fell on Newport River and the land runoff that flowed into the river from upstream produced a marked decline in the salinity of this environment.

In Fig. 7, salinity profiles collected during the subsequent period of low salinity are compared with conditions ten days before the first hurricane. These hydrographic runs were made on August 13 in the

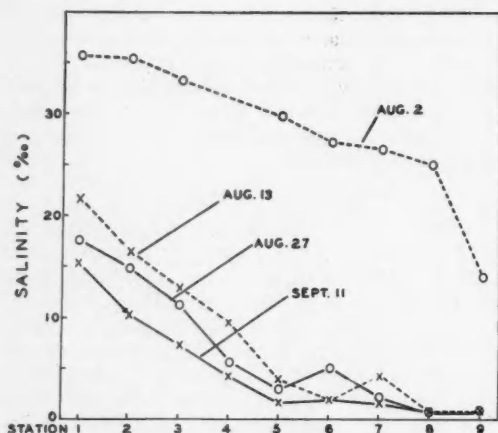


FIG. 7. Salinity profiles, August 2, 13, 27, and September 11, Newport River, 1955. (Hurricane Connie passed on August 12, and Diane, on August 17.)

typical balmy weather following the passage of Connie (on the 12th), on August 27 (ten days after Diane), and September 11 after two weeks marked by more heavy rains (amounting to about 7 inches).

On August 23, six days after the second hurricane, many members of the oyster bed community at White Rock had died. Of 72 oysters and 23 clams dredged then, 36% of the oysters and 87% of the clams had died recently. Their shells were fresh and clean, and several still had intact meats or adductor muscle present. There were none of the xanthid crabs present that would ordinarily devour meats exposed in this manner. Life in the oyster bed was at a low ebb. Recently dead *Anomia*, *Modiolus*, *Crepidula*, and *Membranipora* were observed. The *Bugula*, *Amathia*, and *Styela* on the shells were in poor condition and dying. Since August 4 when 38 species were collected here, half had disappeared or died. After still more heavy rains (Sept. 12), 95 clam "boxes" were dredged in this area, and not one live clam.

At Cross Rock, similar devastation had struck the community. Of 70 oysters collected on August 27, 34% had died recently and several still had meats or adductor muscles present. Several dead *Modiolus* were collected in a similar condition. One recently-dead clam was found. In between the shells were many dead *Odostomia*. There was a marked scarcity of scavengers that might have cleaned up the exposed flesh. Only a few gobies were found, but no xanthid crabs. Of 22 species of oyster associates found there August 2, only 8 had survived.

However, these beds were exposed to still more severe conditions, for Ione struck September 19. Heavy rains had kept salinity down during the intervening period. Salinities remained depressed over a period of at least six weeks. Animals injured by the initial drop in salinity found conditions poor for recovery. Most bivalves that ordinarily exclude and

withdraw from the environment during adverse periods in a state of suspended animation, found that this period exceeded their survival limits. No opportunity arose to restore their internal environment without exposing themselves to adverse conditions.

The prolonged low salinity period was very effective in eliminating many species from the upstream parts of Newport River, and had similarly affected the fauna of down-stream beds. Because little rain fell for some time after Ione, salinity levels rose quickly. Salinity conditions had returned to normal by October 28, but biologically, beds still showed effects of the fresh water that had swept over them. Oyster shells collected at Cross Rock and White Rock had been cleaned an uncharacteristic white. A number of bryozoans and hydroids had returned, apparently carried as planktonic larvae by the inward movement of seawater. With them came a nudibranch, *Catriona tina*, which fed on hydroids at Cross Rock. Their appearance so soon after the general disaster is surprising, though undoubtedly the cleansing of the shells prepared an ideal substrate for the settlement of such forms. The very slow recovery of the Cross Rock fauna was followed in succeeding months.

At Pivers Island, where salinity values usually exceed 30 ‰, salinities off the Duke Marine Laboratory pier dropped to 15 and 10 ‰. Starfish and sea urchins that usually clung to rocks at Shark Shoal had disappeared. Many sessile organisms died and sloughed off, carrying still others with them.

There was a marked decline in the number of species collected at every station during this period. The collections with the smallest number of species at each station were in late August or early September during this period of low salinity.

Other events can occur during hurricanes that would have serious biological effects on an oyster bed. Increased sedimentation may tax an oyster's filtering mechanism so severely that feeding is halted, and respiration and shell movements in general could be affected. Through abnormal wave action or runoff from land, sedimentation may bury an entire bed. Although oyster growth can keep pace with gradual deposits, it cannot do so when deposition occurs in a matter of hours or days. Sedimentation was a serious consequence of a hurricane that hit oyster beds in Louisiana, Mississippi, and Alabama in 1947 (Engle 1948). Although suspended sediments might have been a problem in Newport River, osmotic difficulties would have been a more serious and immediate challenge to any oyster that opened its shell. No major silting effects were noted at any of the beds.

Occasionally, hurricanes open new inlets to the ocean or close others and, in this manner, permanently alter the salinity regime of a coastal area. The fauna of the area would undergo changes accordingly. In terms of an oyster bed, this change might permit the invasion of competitors and predators of the oyster, affect their abundance, or prevent their occurrence.

The hurricanes during this study produced only temporary salinity changes. These changes had severe effects on the fauna of individual beds. The oysters themselves suffered high mortalities, and planted beds in Newport River were severely damaged. Similar mortalities of oysters and associates due to freshets have been reported for several estuarine areas (Beaven 1946, Engle 1945, Galtsoff 1930, Gunter 1952, 1953).

The occurrence of these storms in late summer and early fall had serious effects on life cycles of many species. Recolonization of shell surface cleaned by fresh waters depended, in large measure, upon production of planktonic larvae by animals which survived the devastation. If no adult individuals survived in the immediate area, recolonization would be postponed indefinitely. If the survivors had suffered, the ripening of spawn might be delayed, and those forms with restricted spawning periods or temperatures might not be able to reproduce until a subsequent suitable period. These factors apparently prevented a number of species from making the quick recovery that certain hydroids and bryozoans were able to make in the high salinity period in October.

Repopulation of beds devastated by the low salinities depended largely on the timing of the reproductive season for each species. Using the reproductive periods determined by McDougall (1943) in a "normal year," one can correlate the reappearance of many species with their periods of reproduction.

Many ascidians killed by low salinities were delayed in their reappearance. Low salinity killed adult *Ascidia*, cutting short the fall spawning period. Not until spawning began in May was it collected again. Apparently, the normal mid-winter reproduction of *Styela* was prevented. It reappeared in collections after the start of the spawning period in May. Entire colonies of *Perophora* were killed including the stolons which would ordinarily develop again in April. *Perophora* did not appear in 1956 until mid-August. Sufficient numbers of *Molgula* survived for the fall-winter reproductive period; there was no break in the records of its collection.

Apparently, the bryozoans *Anguinella*, *Bugula*, and *Schizoporella* recovered quickly, in time to repopulate beds in the last part of their reproductive periods (extending into December, January, and November, respectively).

Whereas the barnacles *Chthamalus fragilis* and *Balanus amphitrite* disappeared as a result of the low salinities, the latter species reappeared shortly after salinities returned to normal, for its reproductive period extends through December. *Balanus improvisus* and *B. eburneus* are tolerant of low salinities and were not noticeably affected. Both have late periods of reproduction. *B. improvisus* met less competition than usual for space on clean shell, and prospered.

The hydroid *Tubularia* similarly prospered. It appeared early and disappeared late, although the growth and reproductive period usually extends

from November 30 to June 15. *Eudendrium* disappeared with the onset of low salinities and had not reappeared by October 1956, although spawning usually extends from June to December. *Pennaria* disappeared in August and did not reappear in 1956, although colonies are normally present in summer at Beaufort.

The sponge *Microciona prolifera* normally reproduces in August and September and grows principally during the winter. Low salinities apparently prevented successful reproduction in 1955, for it did not appear in collections until the summer of 1956.

The gastropod *Calliostoma*, which is normally found at the south end of Shark Shoal, was not collected after August 1955. The pyramidellid gastropod *Odostomia impressa* disappeared from upstream stations with low salinities and did not reappear until its 1956 reproductive period.

The echinoderms *Asterias*, *Arbacia*, and *Ophiothrix* disappeared completely from the collections with the onset of low salinities. *Asterias* and *Arbacia* reappeared by May 1956, when *Asterias* was represented by small individuals only. *Ophiothrix* (33 in the last collection before low salinities) did not reappear until September 1956, when 3 were collected.

INDIVIDUAL SPECIES

Distribution relative to salinity has been analyzed for a number of noteworthy species.

Boring sponges. *Cliona celata* was most abundant and was collected at each station. In contrast, *C. truitti* was found only at the two most seaward stations, and was not recorded there for two months after low salinities. *Cliona vastifica* and *C. spirilla* were frequently collected at Shark Shoal; the former was found once at Gallant Point, and the latter was collected as far upstream as White Rock during high salinities. *Cliona lobata* was found at Shuiceway and Gallant Point, but at neither end station. Distribution of *Cliona* species in Newport River and in many South Carolina estuaries (Hopkins 1956e) differs from the pattern found in Louisiana. There *Cliona truitti* and *C. vastifica* are brackish water species, typically penetrating farther upstream than *C. celata* (Hopkins 1956a). It appears that the relative stability of the salinity regime is important in determining which pattern of distribution is found in an estuarine area (Wells 1959b).

Nereid annelids. Both *Nereis occidentalis* and *Neanthes succinea* were represented in almost every collection, but the relative size of the two populations varied in a regular manner. *Nereis* was more numerous in higher salinities, while *Neanthes* was more numerous in low salinities. When the number of *Neanthes* individuals is expressed as a percentage of the nereids collected, an average of 78% were *Neanthes* in the collections at Cross Rock and an average of 21% were *Neanthes* at Shark Shoal. Evidently, *Neanthes* is more successful in brackish waters.

Crabs. In June 1955, blue crabs, *Callinectes sapidus*, were very common on Cross Rock at low tides. They were observed breaking the edges and opening the shells of oysters to get to the meats inside. With approximately four crabs to every 6 m of reef edge, they were more numerous on this occasion than at any other collection, although crabs were observed at every station. *Callinectes* can penetrate far into brackish and even fresh waters (Churchill 1919, Gunter 1938, Odum 1953), well beyond the limit of this study. It is recognized as a serious predator of oysters, particularly young oysters (Lunz 1947). In certain areas, blue crabs may effectively limit oyster distribution to places where some protection from them is to be found (Marshall 1954). Adults are not permanent residents of the oyster bed, but only influents. On the other hand, young *Callinectes* may occupy burrows in soft bottoms between oyster clusters.

Panopeus herbsti, a xanthid crab, hides in clusters of oysters and in intact valves of dead oysters. It was collected at all stations. Although larger individuals have been observed feeding on small oysters (MacDonald 1940, McDermott & Flower 1953), there is no evidence that *Panopeus* is a serious predator (Ryan 1956). *Eurypanopeus depressus*, the most abundant xanthid crab collected, was taken at every station. It is a scavenger, usually hiding under sponges and in oyster clusters.

Pinnothereos ostreum was generally found only at Shark Shoal and Sluiceway, although one specimen was collected at White Rock during the period of very high salinities. Young females (carapace width to 2 mm) were collected in October 1956, and free-living hard stage males were collected during the winter. The females of this species live as commensals or parasites in the mantle cavity of oysters where they collect food from mucus strands formed on the oyster's gills (Stauber 1945).

Clibanarius vittatus, the striped hermit crab, is one of the most active scavengers of the oyster bed. It is common at Sluiceway and Gallant Point, and was once collected at White Rock. *Pagurus longicarpus*, a small hermit crab, was also found as far up the river as White Rock, inhabiting sandy bottoms, and probably finding food and shelter among the shells.

Pelecypods. Although the occurrence of the hard clam, *Mercenaria mercenaria*, has been related to high salinities in Core Sound (Chestnut 1951), they have been found as far upstream as Cross Rock. They burrow into the substrate, often in shelly bottoms near oyster beds (Wells 1957). This abundance is probably due to the favorableness of shell as a substrate for setting of larvae.

Modiolus demissus, the ribbed mussel, was found at every station attached in the upper intertidal zone to clusters of oysters, rocks, or *Spartina* roots. *Brachiodontes exustus*, a small mussel, attaches in great numbers to pilings, rocks, and shells in the in-

tertidal zone as far up Newport River as Gallant Point.

Except for a few juvenile specimens collected at Gallant Point, the small clam *Chione cancellata* was found only at Sluiceway where it was common on the surface of a mud or shelly substrate between oysters. Metamorphosing larvae probably utilize shells for their initial attachment, as do *Mercenaria* larvae.

Gastropods. *Odostomia impressa*, a small pyramidelid, was collected at all stations until the low salinity period that accompanied the hurricanes. It then disappeared from all stations except Shark Shoal and Sluiceway, not reappearing at upstream stations until the summer reproductive period of 1956. MacDonald (1940) thought this species fed on algae. However, like other Pyramidellidae, *O. impressa* has adopted an ectoparasitic habit, feeding upon blood and tissue debris sucked from the mantle of *Crassostrea* (Hopkins 1956b, Wells 1959a). They are numerous on oyster beds, gathered in crevices in oyster clusters.

Urosalpinx cinerea, the Atlantic oyster drill, was commonly found as far upstream as Gallant Point. Small individuals were more abundant at Shark Shoal and Sluiceway, while larger ones predominated at Gallant Point. It is a well-known oyster predator, perforating the shell to feed on its prey (Carriker 1955). It will eat thin-shelled mussels, then oyster spat, in preference to adult oysters. Federighi (1931b) estimated that a drill can kill 30 to 200 oysters in a season at Beaufort, depending on their size. *Urosalpinx* is one of the most important predators of oysters.

Fasciolaria hunteria, a large predaceous gastropod, was frequently collected at Shark Shoal and Sluiceway. This species is a natural predator of the Atlantic oyster drill (*Urosalpinx cinerea*), but will feed on a variety of gastropods and pelecypods, including the oyster (Wells 1958).

Thais floridana, the Gulf oyster drill, was collected in the intertidal zone at Shark Shoal and occasionally at Sluiceway. It is an important oyster predator on the Gulf Coast (Burkenroad 1931, Butler 1954). However, because it prefers thin-shelled mussels to oysters, an abundance of mussels may protect nearby oysters from attack; *Thais* may help oyster culture by keeping down the numbers of mussels which must be culled from oysters before marketing (Burkenroad 1931).

Relatively few conchs, *Busycon carica*, were collected in oyster beds, and all of these were taken at Sluiceway. They occur primarily on sand flats, feeding mostly on hard clams. However, Carriker (1951) found that *Busycon* would eat thinner-shelled forms, such as mussels and oysters, before eating hard clams.

Nassarius vibex, a prosobranch gastropod, was found in association with oysters living on sand at every station but Cross Rock. It is a scavenger. *Cantharus tinctorius* was commonly found on encrusted rocks and oysters at Shark Shoal, and occasionally at Sluiceway. There is no evidence that it feeds on

oysters. Another gastropod, *Cerithium floridanum*, was collected at Shark Shoal and at Pivers Island, near Sluiceway. It feeds on algae and various aquatic plants (Morris 1951).

Echinoderms. Except for one specimen collected at Sluiceway, starfish (*Asterias forbesi*) were found only at Shark Shoal below mean tide levels. This species is particularly troublesome to the oyster industry in Long Island Sound where it is responsible for destroying large numbers of oyster spat (Galtsoff & Loosanoff 1939). It will also eat adult oysters, other pelecypods, gastropods, and small crustacea.

Arbacia punctulata was abundant near and below the low tide mark at Shark Shoal, and common at Sluiceway during normal salinity periods. While feeding on algae and encrusting organisms, sea urchins may eat oyster spat that have set on oyster shells. In the Beaufort area, the population of another sea urchin, *Lytechinus variegatus*, is centered in deeper water (over 5 ft) on shell bottoms in the sounds. Only a single specimen was found at Sluiceway. It feeds on algae and other organisms that encrust shells.

SALINITY TOLERANCE

Distribution records alone do not fix the relationship between salinity and distribution as cause and effect. Yet many workers have relied solely on observed distribution patterns without resorting to a study of physiological tolerances of the species involved. For this study, salinity tolerance experiments were performed on 20 major species to provide a basis for judging the importance of salinity to their distribution.

Single invertebrate species have been the subject of a number of salinity tolerance studies—*Urosalpinx cinerea* (Engle 1953, Federighi 1931a, Galtsoff et al. 1937, Sizer 1936, Stauber 1943), *Thais haemastoma* (Schecter 1943), *Nereis diversicolor* (Smith 1955), *Asterias forbesi* (Loosanoff 1945), *Crassostrea virginica* (Loosanoff & Smith 1949), *Limnoria lignorum* (Miller 1926), *Teredo navalis* (Blum 1922, Kofoid & Miller 1927), *Clibanarius tricolor* (Kunkel 1933), and *Brachiodontes recurvus* (Allen 1960). Only in rare instances are the results strictly comparable, for the salinity experiments have been conducted under a variety of experimental conditions.

Pearse (1928a, 1928b) tested the salinity tolerance of a number of annelids and decapods, expressing the results in terms of survival time in different dilutions of sea water. He also tested in a similar fashion the tolerance of 21 coral-reef species at the Dry Tortugas (Pearse 1929). However, the fauna of a coral reef is never exposed to the low salinities typical of estuarine situations. The ability to tolerate salinity reductions would not have the selective advantage in such an environment that it would have in an estuary. Few species at Tortugas showed such an ability.

At Beaufort, Pearse (1936) tested salinity tolerance in 45 estuarine species. Again results are ex-

pressed as survival time in various dilutions of seawater, indicated as fresh water, $\frac{1}{4}$, $\frac{1}{2}$, $\frac{3}{4}$, and full seawater. With this rating system, it is difficult to rank individual species for comparison purposes on the basis of their salinity tolerance. Pearse tried to correlate his results with distribution, but they did not permit the establishment of relative salinity death points. During the course of his experiments, the salinity of "full seawater" varied somewhat, and often the number of experimental animals was insufficient, allowing individual variability to have a greater influence on the final values.

Topping & Fuller (1942) tested the ability of 14 estuarine species to acclimate to low salinities by gradual dilution. Because they worked with few animals in each species, kept no controls, and ran experiments for more than 30 days without feeding, their results are open to question. Moreover, shortcomings in their hydrographic data weaken any correlation with distribution.

METHODS

For this study, 20 species were selected for experimentation on the basis of their abundance on the oyster beds and the convenience with which they could be collected and maintained in the laboratory. Series of 10-liter all-glass aquaria were filled with different dilutions of seawater. Usually, there were 16 aquaria with solutions ranging from 0 to 30 ‰ salinity, by 2 ‰ intervals (i.e., 0, 2, 4, 6, . . . ‰), made up by diluting seawater. Four liters of solution were placed in each aquarium, and aeration was provided. Each aquarium was covered loosely to reduce evaporation and consequent changes in salinity. Water temperature was nearly uniform in all aquaria and followed air temperatures in the laboratory.

The only factors which differ in the series of aquaria were salinity and hydrogen ion concentration. Experimental pH values corresponded with pH values found accompanying similar salinities in Newport River. Because hydrogen ion concentration is related to salt content, the separation of these factors would be very difficult; and since they vary together in nature, their separation seems undesirable.

These experiments were conducted June to August 1955 and June to September 1956 at relatively high summer temperatures. Experimental animals were usually collected near the Duke Marine Laboratory, except for specimens of *Odostomia* collected at Cross Rock and those of *Lytechinus* dredged in Bogue Sound off Morehead City. For each species, the number of experimental animals placed in each aquarium depended on their size and availability. For each experiment, an equal number was placed in each aquarium. Every effort was made to distribute size variations evenly among all aquaria. Ordinarily, each experiment was terminated after 5 days. Each day, dead specimens were removed and recorded. Usually all specimens survived above a certain salinity, and all specimens below that salinity died. The

survivors in higher salinities served as controls for the experiment, for salinity was the only factor (other than pH) that differed.

The salinity which most clearly separated living from dead animals after 5 days was termed the "salinity death point" for that species. When all or almost all individuals survived in one salinity and higher salinities and when all or almost all died in the next lower salinity, the salinity mid-way between the two solutions was accepted as the salinity death point. If as few as 10% of the individuals at a given location survive the stress of a period of low salinity, they can repopulate the area. Therefore, to have ecological significance this salinity death point should lie below the 10% survival level. Usually any individuals which were still alive below the salinity death point showed signs of injury or did not exhibit normal behavior by the fifth day.

In this manner, the results are expressed as a limiting salinity for 5 days' exposure, rather than a survival time in particular dilutions of seawater. Such a salinity death point provides a statistic by which species can be compared with ease, and the results can be compared to results obtained in other areas for the same species.

For gastropods, the lack of any response to stimulation of siphon or foot was the criterion used for death. For pelecypods, gaping valves and no response to stimulation of the exposed foot; and for decapods, lack of movement or muscular tonus were criteria. The loss of movement and attachment served as criteria of death in echinoderms.

Those species which have the ability to adjust to rapid changes in salinity would also have the ability to adjust to gradual changes such as would be used in acclimation experiments, and might survive at a lower concentration of salts, if they were gradually introduced. Presumably, their relative success in acclimating would equal or exceed their relative success in surviving at reduced salinities when the change is sudden. From a practical point of view, the time required for acclimation experiments would sharply curtail the number of species that could be studied.

Although many arthropods appear to tolerate lower salinities at higher temperatures (Panikkar 1951, Pearse & Gunter 1957), this is not true for molluscs such as the oyster drill. At low temperatures, Delaware Bay oyster drills can survive low salinities that result from heavy spring runoff, salinities which would be fatal at high summertime temperatures (Stauber 1943, reported by Carriker 1955). Where extremely low salinities may occur at high temperatures, as in coastal North Carolina under the influence of tropical storms, these periods of low salinity probably are more important in determining upstream limits of species than are wintertime lows. The low salinities of winter and spring were not as extreme as the low values recorded after the hurricanes. Thus, the experimental conditions, including high temperature, simulate the stresses that ap-

parently determine the limits of these species in Newport River.

RESULTS

Table 7 presents the salinity death points determined for each species with data on experimental conditions.

TABLE 7. Conditions and results of salinity tolerance experiments.

Species	Length range (mm)	Number per salinity interval	Temperature range (°C)	Salinity Death Point (o/oo)
Gastropods:				
<i>Nassarius vibex</i>	11-17	13	22.8-26.2	9
<i>Thais floridana</i>	47-78	4	28.0-28.5	9
<i>Odotostoma impressa</i>	1-4	20	28.0-30.0	11
<i>Urosalpinx cinerea</i>	12-30	20	26.1-28.1	11
<i>Busyon carica</i>	41-86	4	26.0-26.5	11
<i>Cerithium floridanum</i>	24-48	6	26.0-26.5	13
<i>Fasciolaria hunteria</i>	38-91	3	27.5-28.5	17
<i>Cantharus tinctus</i>	15-30	16	26.5-27.0	18
<i>Thais veligers</i>	—	50	25.0-27.5	9
<i>Cerithium veligers</i>	—	30-70	23.5-26.0	21
Pelecypods:				
<i>Mercenaria mercenaria</i>	30-123	4	25.3-27.5	(0)
<i>Modiolus demissus</i>	62-98	6	28.2-28.9	5
<i>Crassostrea virginica</i>	20-117	6	26.0-28.0	7
<i>Brachidontes exustus</i>	8-22	25	24.5-27.5	13
<i>Chione cancellata</i>	18-40	11	27.0-28.5	19
Decapods:				
<i>Panopeus herbsti</i>	20-40	4	24.0-27.5	3
<i>Eurypanopeus depressus</i>	4-17	11	25.0-27.5	3
<i>Libinia vittatus</i>	—	2	26.0-26.5	5
<i>Pagurus longicarpus</i>	—	18	22.8-26.2	9
Echinoderms:				
<i>Asterias forbesi</i>	55-120	4*	23.5-26.0	17
<i>Arbacia punctulata</i>	47	2	27.5-28.7	19
<i>Lyttechinus variegatus</i>	48	1	27.5-28.7	23

* 16 specimens in 14, 16, and 18 o/oo dilutions.

In low salinities, *Thais* withdrew into its shell, closing the operculum until an adjustment to the experimental conditions had been made or death occurred. Death was usually accompanied by a swelling of tissues around the operculum. Schecter (1943) found *Thais* had difficulty righting itself at 10 ‰ and below, and eventually lost this ability after 40-50 hrs. His results fit the pattern of mortality in the current experiment although his animals were acclimated to 14 ‰ salinity. Butler (1954) noted that *Thais* acclimated to 20 ‰ survive at 10 ‰ without ill effects although animals adjusted to 35 ‰ are seriously injured at 15 ‰. In the current experiment, animals acclimated to 35 ‰ could survive to 10 ‰ although they initially showed an unfavorable response.

Federighi (1931a) arrived at a "salinity death point" of 15.6 ‰ for *Urosalpinx* in the Beaufort area. This figure is midway between a lethal salinity, where at least 50% of the drills died in 8-10 days, and a survival salinity, where not more than 10-15% died. Federighi's "lethal salinity" which approximates the definition of salinity death point used here, ranged from 12.8 to 16.6 ‰, considerably higher

than the 11 ‰ value I obtained (Table 7). Carriker (1955) suggested that the discrepancy might be due to the toxic effects of metal screens used by Federighi to keep his drills immersed. Otherwise, conditions in his experiments were similar to those listed in Table 7 for *Urosalpinx*.

Carriker (1955) compiled a list of salinity values below which drills apparently do not survive at summer temperatures (Table 8). Stauber's concept of physiological races in *Urosalpinx* (Stauber 1950) would explain the differences in individual populations, but the current results suggest that the salinity death point for Beaufort drills is much lower than Federighi's value and more in line with values obtained for other populations. The value of 11 ‰, arrived at in this experiment, does not seem an unlikely deviation, for Delaware Bay drills can survive salinities of 7 or 8 ‰ for weeks at temperatures below 20°C (Stauber 1943).

TABLE 8. Salinity values lethal to *Urosalpinx cinerea* at summer temperatures. From Carriker (1955).

Location	Salinity	Reference
Peaufort	17 ‰	Federighi 1931a
Hampton Roads	12 ‰	Federighi 1931a
Long Island Sound	16 ‰	Engle 1953
Delaware Bay	12-15 ‰	Sizer 1936, Galtsoff et al 1937, Stauber 1943

Because few deaths occurred in the *Mercenaria* experiment, it was extended through nine days. Even then, no salinity value qualified as a death point, for only three small clams died in scattered dilutions.

Churchill (1920) noted that oysters cannot stand densities lower than 1,007 for indefinite periods. This would correspond to a salinity of about 9 ‰. He did not include the authority for this claim, and it seems likely that it was an estimate based on oyster distribution or mortalities associated with low salinities. Other workers have apparently taken this approach, and, as a result, comparative salinity tolerance data on *Crassostrea* are scarce. Heavy mortalities occurred in upper Chesapeake Bay when salinities fell below 10 ‰ for a prolonged period in 1945 (Engle 1946). Loosanoff & Smith (1949) found that oysters can be acclimated to salinities as low as 7.5 ‰. Minimum salinities for feeding and life were simultaneously shifted. Gunter (1953) noted that oysters can survive salinities as low as 2 ‰ for a month, or fresh water for several days, at low temperatures. However, at high temperatures such acclimation may not be effective.

Loosanoff (1945) also found the salinity death point for *Asterias* between 16 and 18 ‰, although it was not until one month had elapsed that deaths occurred in 16 ‰. The present experiment was conducted at a higher temperature, which would be expected to hasten death, and upon smaller specimens, which are typically more susceptible to osmotic

disturbances. Loosanoff found the normal salinity threshold was stable, whether salinity was reduced gradually or abruptly.

Both *Modiolus* and *Brachidontes* attached to the sides of aquaria by their byssal threads in salinities above 14 ‰.

Cannibalism was noted for *Fasciolaria* and most of the decapods at high salinities. There was no confusion with salinity as a cause of death however, for all feeding was inhibited at lower, near-lethal salinities.

Salinity tolerances of the pelagic veliger larvae of *Thais* and *Cerithium* were also tested. These larvae were placed in syracuse dishes containing 10 ml of solution for each salinity interval. *Thais* veligers exhibited the same tolerance to low salinities that was found in adults, although the species is not found far upstream in lower salinity waters. This result ruled out the possibility that a high larval death point serves as the limiting factor in the penetration of *Thais* up Newport River. It seems most likely that larval metamorphosis might be the critical stage in the life of *Thais* that prevents its invasion of less saline waters. *Thais* appears to be salinity limited because it was collected only at stations near the ocean. In North Carolina oyster beds, it is an important oyster predator only at Ocracoke, where the beds are located in more saline waters near the inlet (Chestnut, pers. comm.).

Cerithium veligers, on the other hand, showed a salinity death point significantly higher than that of adults. Apparently, it is the salinity dependence of the veliger rather than of the adult which limits the distribution of *Cerithium floridanum* in Newport River. This fits the classical concept of reproductive and larval stages being the most sensitive in the life history of an animal. "We have to focus our attention upon the most sensitive stages within the life cycle of the animal. These stages . . . will normally be found during the breeding period and larval development" (Thorson 1946). The larval salinity death point for *Cerithium* is a better indicator of the salinity tolerance of the species, and it will serve that purpose in the following comparisons.

Eleven of these species were tested by Pearse (1936). In Table 9, the ranking of salinity death points is compared with a ranking based on Pearse's data. Some interesting comparisons can be made between the phylogenetic groups. Generally, gastropods show a broad intermediate range of salinity death points; pelecypods show a very broad range from very low to very high salinity death points; decapods, very low death points; and echinoderms, very high salinity death points. Topping & Fuller (1942) drew up a similar sequence of phyla in relation to their survival ability in low salinities, ranging from arthropods (5 species) with the best survival, through annelids (2 species), molluscs (3 species), nemerteans (1 species), and echinoderms (1 species), to coelenterates (2 species) with the poorest survival.

TABLE 9. Comparison of salinity death points with results obtained with these species by Pearse (1936).

Species rank in order of salinity death point	Rank according to survival time in $\frac{1}{2}$ seawater (Pearse)	Rank according to survival time in fresh water (Pearse)
1 <i>Mercenaria</i>	1	1
2 <i>Panopeus</i>	1	6
2 <i>Eurypanopeus</i>	1	5
4 <i>Modiolus</i>	1	2
4 <i>Clibanarius</i>	1	7
6 <i>Crassostrea</i>	1	4
7 <i>Pagurus</i>	8	7
8 <i>Urosalpinx</i>	9	7
9 <i>Fasciclaria</i>	11	11
10 <i>Chione</i>	7	3
11 <i>Arbacia</i>	10	10

Pearse (1936) also cited arthropods as excelling in their ability to tolerate extreme variations in salinity.

The relative tolerance of phylogenetic groups can be explained on the basis of mechanisms of protection and adjustment that function in low salinities. The following structural mechanisms protect tissues from osmotic difficulties encountered in low salinity waters: *Gastropods*—The operculum and shell into which a snail withdraws are only partially effective in sealing off the external aquatic medium, but they do reduce the surface across which water would diffuse into the tissues. *Pelecypods*—Those species in which the shell margins are contiguous throughout their length can effectively shut out the external medium. The animal must rely upon its store of glycogen for anaerobic respiration while closed, and the amount in storage determines the length of time that the animal may remain closed. Once the valves open, the tissues are in direct contact with the medium. *Decapods*—Generally, the chitinous exoskeleton prevents water exchange across surfaces except those specialized for respiration, the gills. *Echinoderms*—The dermis is in direct contact with the aquatic medium, and the calcareous endoskeleton is quite porous; there is no structural protection from osmotic disturbances.

Physiological mechanisms of protection against the effects of low salinity usually involve some degree of osmoregulation. Although fresh-water molluscs show a degree of osmoregulation, marine molluscs apparently show little or none. Decapods may possess quite effective powers of osmoregulation; of the decapods tested, at least the two xanthid crabs probably osmoregulate. However, there is no osmoregulation among echinoderms (Beadle 1957). Apparently, the differences in specific salinity death points within these groups are largely due to differences in the ability of species to withstand changes in the internal environment, that is, to differences in osmoadjustment.

Three different mechanisms of salinity death seem possible:

1) In an animal which osmoregulates, oxygen is required for the work involved, and when the sum of

this osmoregulatory demand and normal respiratory demand exceeds the oxygen supply, death may follow. At higher temperatures death might occur at higher salinities, because the metabolic demand for oxygen would be greater, while a depressed metabolism at lower temperatures would not make such a demand on the oxygen supply (Schlieper 1929, Beadle 1931). However, Potts (1954) has indicated that the oxygen used by osmoregulation is but a small fraction of total oxygen consumption, and Krogh (1939) and Gross (1957) suggest that increases in oxygen consumption in low salinities may be due to factors other than osmoregulation.

2) In an animal which adjusts to a diluted internal medium, there is a critical dilution beyond which normal life processes cannot take place. The concentration of salts and other substances may become diluted below a critical value which is essential for life. Reduced salt concentrations probably cause irreversible changes in permeability of membranes (Schecter 1943, Loosanoff 1945).

3) Osmotic disruption of tissues may occur, leading to injuries extensive enough to cause death.

Sumner (1906), Adolph (1925), and Beadle (1943) agree that the loss of essential salts is the cause of death of marine animals placed in dilute seawater. Such a mechanism probably is the cause of death in most of these experiments. Only detailed investigations into the physiology of each species could determine the cause of death with certainty.

In several experiments, particularly with *Mercenaria* and *Crassostrea*, the smaller, young animals died before larger specimens. In salinity tests upon *Clibanarius tricolor*, Kunkel (1933) found a similar size distribution of the survivors at near-critical salinities. However, Topping & Fuller (1942) and Pearse (1929) generally found the smaller members of each species better able to adapt and survive in low salinity. The observed differential mortality can be attributed to changes in the relation of surface to volume as an organism grows larger. Relatively, there is a greater surface area in small animals than in large ones of the same species, the surface increasing as the square of a linear dimension, while the volume increases as the cube of a linear dimension. The amount of water moving into an animal depends on the surface exposed, while the amount of internal medium (blood) that is diluted depends on the volume of the animal. Any effect of this differential mortality with size was reduced to a minimum by distributing size groups evenly among all salinities.

DISCUSSION

In Table 10, the 20 species for which salinity death points were determined are ranked, first according to their distribution in Newport River, and secondly according to their tolerance for low salinities as determined in experiments. Abundance and frequency of collection were taken into account in ranking species that are apparently limited at the

same station. The two columns are very similar. With two exceptions, each species shows a salinity tolerance that corresponds very well to the relative position of its upstream distribution limit. The probability of finding such a positive correlation ($\gamma = 0.83$ or $\rho = 0.857$) between these rankings due to chance is less than 0.001; statistically there is a very significant correlation between salinity tolerance and distribution. In view of these results, salinity is probably limiting to 19 of 20 species tested. At this rate, 15 of the 303 species found in the oyster bed community would not be directly limited by salinity. With a large group of experimental species

TABLE 10. Ranking of 20 species of estuarine animals on the basis of their distribution limits and tolerance to low salinities. (The most tolerant species are listed first.)

Distribution	Tolerance
1 <i>Mercenaria</i>	1 <i>Mercenaria</i>
2 <i>Panopeus</i>	2 <i>Panopeus</i>
3 <i>Eurypanopeus</i>	3 <i>Eurypanopeus</i>
4 <i>Modiolus</i>	4 <i>Modiolus</i>
5 <i>Crassostrea</i>	8 <i>Clibanarius</i>
6 <i>Nassarius</i>	5 <i>Crassostrea</i>
7 <i>Pagurus</i>	6 <i>Nassarius</i>
8 <i>Clibanarius</i>	7 <i>Pagurus</i>
9 <i>Ostomia</i>	17 <i>Thais</i>
10 <i>Urosalpinx</i>	9 <i>Ostomia</i>
11 <i>Brachidontes</i>	10 <i>Urosalpinx</i>
12 <i>Busycon</i>	12 <i>Busycon</i>
13 <i>Fasciolaria</i>	11 <i>Brachidontes</i>
14 <i>Chione</i>	13 <i>Fasciolaria</i>
15 <i>Arbacia</i>	19 <i>Asterias</i>
16 <i>Cantharus</i>	16 <i>Cantharus</i>
17 <i>Thais</i>	14 <i>Chione</i>
18 <i>Cerithium</i>	15 <i>Arbacia</i>
19 <i>Asterias</i>	18 <i>Cerithium</i>
20 <i>Lytechinus</i>	20 <i>Lytechinus</i>

to use as reference, considerable confidence can be placed in such an estimate.

In earlier discussion on *Thais*, it has been pointed out that low salinity probably limits the distribution of *Thais* by operating on metamorphosing larvae, rather than on adults. The oysters, barnacles, and mussels which serve as food for *Thais* extend far upstream, so that the availability of food organisms would not be limiting; and if there were any change in levels of competition and predation in brackish waters, these factors should be of less importance there than in the high salinity areas where it lives. Alternatives to salinity as the limiting factor seem unlikely.

Clibanarius is dependent on large gastropods (*Busycon*, *Fasciolaria*, or *Polinices*) for the shell which it occupies. A scarcity of these shells in lower salinities may serve to limit its penetration upstream. Also, *Clibanarius* may require higher salinities for normal spawning activity, as do many other decapods. In the absence of swimming ability in adults, such a reproductive requirement might effectively restrict its penetration upstream.

The salinity death point obtained for *Lytechinus* must be considered provisional because of the small number of individuals involved in the tests. Field observations had indicated that *Lytechinus* is more sensitive to low salinities than *Arbacia*, and the results support this view. Its salinity death point seems reasonable in relation to those obtained for other species.

Although few deaths occurred among hard clams kept in low salinities for 9 days, *Mercenaria* cannot survive such conditions indefinitely. Because it depends on how long a clam can remain closed, salinity death becomes a function of the stored glycogen available for anaerobic utilization. Eventually, a clam must open and expose its tissues to the surrounding medium and suffer the consequences. During the low salinity period caused by the hurricanes, this occurred on a large scale, and many clams and oysters died in upper Newport River. *Mercenaria* showed a higher mortality than did oysters in the same area, and probably are not able to survive prolonged low salinities as well as oysters.

Apparently few *Modiolus* died at Cross Rock during this period. Their situation in the upper part of the intertidal zone may have been their salvation. *Modiolus* are not exposed there to the salinity minima which occurred at low tides; instead, they come into contact with the more saline water that returned with high tides.

No other factor rivals the importance of salinity in limiting the upstream penetration of estuarine species. Although upstream stations typically show greater extremes in water temperature, animals associated with oysters on Shark Shoal are subjected to more extreme variations during their exposure at low tides. There is, then, no greater range of temperature tolerance required for life in the upper part of the river. Water color has no apparent biological effect upon these animals. Turbidity upstream conceivably could prevent invasion by certain species, possibly by interfering with the efficiency of respiratory or feeding mechanisms. In reality, all stations showed considerable amounts of suspended matter; at no station is the water really clear. At any rate, turbidity is not likely to affect the distribution of many of the 303 species collected. Hydrogen ion concentration acts in conjunction with salinity; only below 20 ‰ is it altered, and in the field, a separation of its possible effects from those of salinity is impossible. All stations were exposed to strong tidal currents, and individual differences between stations probably are not great enough to cause species differences. The confinement of this study to shell bottoms greatly limited any effects of bottom type upon the pattern of distribution. Because there was sand near each station but Cross Rock, any influence it might have had upon the pattern of distribution was reduced to a minimum.

The distribution of certain species could be limited by their reliance for their food supply on a particular species or group of species whose distribution in turn

might be determined by salinity, substrate, or some other factor. Competition or predation by other species may effectively reduce the abundance of a species, but this mechanism seems more likely to operate on the ocean side of the center of distribution of an estuarine species.

For certain species, the degree of larval mobility may limit the powers of invasion or re-invasion. This would be of importance only in those species which produce a non-pelagic larval stage, such as certain gastropods whose eggs develop to metapohosis within a capsule (e.g., *Urosalpinx*, *Eupleura*, *Fasciolaria*, and *Busycon*). Such a mechanism may retard invasion, but it is unlikely to prevent it altogether. In the case of the oyster drill *Urosalpinx*, juvenile specimens may attach to floating vegetation or debris and be transported to other areas, thus compensating for the lack of planktonic dispersion of larvae (Carriker 1957).

All these factors may be acting simultaneously on the animals of the oyster bed community, but their separate effects were not determined. By an investigation of the single factor salinity, close correspondence has been shown between experimental results and the facts of distribution. Detailed analyses of other factors might show examples of cause-and-effect relationships to distribution, but the greatest proportion of species falls into a salinity-limited distribution pattern. Indeed, salinity seems clearly to be the most important single factor limiting the upstream penetration of oyster associates.

Characteristic assemblages of estuarine animals have been cataloged for many areas, attributing the observed distribution patterns to the effects of salinity. For example, Parker (1956, 1959) and Ladd (1951) cataloged the characteristic assemblages of invertebrates in Texas and Louisiana, using salinity as a determinate factor. However, experimental corroboration of the assumed relationship has rarely been attempted. The close correlation between salinity tolerance and distribution found in this study provides a firm basis for regarding salinity as an effective limiting factor, responsible for establishing the upstream limits of many estuarine animals.

Such studies of distribution under relatively stable salinity conditions are supplemented by studies made under conditions of temporarily altered salinities. Gunter (1955) and Parker (1955) have followed changes in typical estuarine communities at times of drought when salinities are elevated; and Beaven (1946), Engle (1945), Galtsoff (1930), and Gunter (1952, 1953) have followed changes during periods of high river flow or high runoff when salinities are reduced. In addition to these studies of temporary changes caused by meteorological phenomena, Reid (1955, 1956, 1957) has been able to follow faunal changes related to changes in the salinity regime induced by the creation and closing of an inlet on the Texas coast. When considered together, this body of information could be used to predict the faunal composition of an estuarine area

under a particular set of salinity conditions, and to predict changes in estuarine fauna to be expected with an alteration of the environmental salinity. Such predictions would be useful for evaluating the effects of both short-term changes and long-term alterations in the salinity regime—such as those associated with a shift in climate or the relatively permanent opening or closing of an inlet. In higher salinities, more species occur on an oyster bed and, among them, more competing or predatory organisms. Lower salinities would reduce the number of species and probably eliminate some competing or predatory forms. Allowing sufficient time, such changes are to be expected as a direct result of alteration of the salinity regime. In this manner, one should be able to anticipate the desirable or adverse effects of a newly created inlet upon oyster bottoms, or the biological advantage of closing an existing one. Similarly, a knowledge of relationships between the distribution of estuarine species and their salinity tolerance is invaluable to paleontologists concerned with paleoecology and the interpretation of fossil assemblages. A great number of species in a fossil oyster bed would be indicative of higher (more oceanic) salinities; few species would be indicative of lower salinities.

The observed distribution of species illustrates the widely-recognized concept that species numbers decline and abundance within each species increases as conditions become less favorable for living organisms (Thienemann 1920). As Gunter (1950) has pointed out, estuarine faunas are almost wholly marine; and for marine organisms, the invasion toward fresh water is an approach to much less favorable osmotic conditions. Of the abundant species collected in this study, only one isopod could tentatively be classified as a truly estuarine, non-marine species. No influx of fresh-water species replaces the larger number of marine species eliminated in lower salinities.

Except for the blue crab, serious predators of the oyster are relatively limited to more saline waters. *Thais*, *Urosalpinx*, *Asterias*, *Busycon*, and *Fasciolaria* were limited in their distribution to the two or three stations closest to the inlet. A zone of brackish water remains where the oyster flourishes without predation by these species, where natural oyster reefs develop, and where commercial oyster culture is pursued. In Newport River this zone lies between Core Creek and the vicinity of Cross Rock.

In the most saline areas, predators are numerous. They seem numerous enough to determine the local distribution of the oyster, by preying upon those which set below the low tide mark. In intertidal zones, on the other hand, periodic exposure apparently discourages predatory activities of these species, permitting a survival of oyster spat there. Predatory activity in high salinities may be at least partially responsible for differences in distribution between *Crassostrea* and *Ostrea* (Wells & Gray 1960a). If *Crassostrea* is more attractive than, or preferred to, *Ostrea* by these predators, as has been found for

Fasciolaria (Wells 1958), then by their selective predation on *Crassostrea* they may produce the differences in zonal distribution characteristic of these two species of oysters. Newcombe (1935) and Paris (1960) have suggested that the predation of murieid gastropods and other predators is similarly responsible for maintaining the distinct lower limit to littoral *Mytilus* communities.

For many of the species collected in oyster beds, their role in this community is poorly understood. Final classification as herbivore, carnivore, or scavenger must await detailed study of feeding habits. The recent recognition (Hopkins 1956b) of *Odostomia impressa* as an oyster ectoparasite is a notable example of a recent discovery in this field that emphasizes the superficiality of our knowledge in the past.

Undoubtedly, larval tolerance to reduced salinity may be of equal or even greater importance than adult tolerances in limiting the penetration of certain species upstream. To evaluate the importance of larval requirements, larval and adult death points should be compared for a number of estuarine species.

Thus, many questions remain unanswered which must await the results of future research on the fauna of oyster beds and its relation to salinity.

SUMMARY

In this study conducted in the Beaufort, N. C., area, 1955-1956, the distribution of oyster associates has been compared with physical factors, particularly salinity. Three hundred and three species were collected. The number of species declined upstream and bore a direct relationship to salinity conditions. Mortalities due to hurricanes and the subsequent recovery of oyster beds were followed.

Twenty species were tested in the laboratory for tolerances to low salinities. The ranking of their salinity death points was compared with distribution of these species in Newport River. Only two species showed wide deviations from the distribution expected on the basis of their salinity death points. It is concluded that a great majority of the species of the oyster bed community are limited in their upstream penetration by salinity.

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ANALYSIS OF THE FOREST FLOOR HABITAT WITH A STRUCTURAL CLASSIFICATION OF THE LITTER OR L LAYER

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TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	267	DISTRIBUTIONAL PATTERN	274
STUDY AREAS	268	THICKNESS OF THE FOREST FLOOR STRATA	276
Beech-Maple Forest	268	EFFECT OF TOPOGRAPHY AND HERBACEOUS	
Oak-Pine-Aspen Forest	269	VEGETATION ON DEPTH AND DISTRIBUTION	
Oak-Hickory Forest	269	OF LITTER	277
Swamp Hardwood Forest	269	TOTAL VOLUME OF HABITAT	278
Montane Rain Forest	270	COMPRESSION CHARACTERISTICS AND	
NOMENCLATURE AND CRITERIA USED IN		INTERSTITIAL SPACE	279
CLASSIFICATION OF LITTER TYPES	270	RELATION BETWEEN DEPTH AND COMPRESSION ..	281
DESCRIPTION OF CLASSES AND TYPES OF LITTER ..	271	SEASONAL CHANGE IN LITTER DEPTH	281
Class I	271	DISCUSSION	281
Class II	272	SUMMARY	282
Class III	273	LITERATURE CITED	283
LEAF THICKNESS	273		

INTRODUCTION

During a study of amphibians in Venezuelan Montane Rain Forest, I was impressed with the need for a classification of the litter on a structural basis that would permit comparisons between different areas and vegetational formations. Such a classification is particularly desirable in tropical areas where it is difficult to characterize a forest type by one or two dominants which contribute the majority of leaves to the litter. In many places it is almost impossible to identify leaves from the litter even as far as family. This difficulty is compounded by the similarity of the leaves of many species. In temperate regions such phrases as "beech-maple litter" convey a rather good idea of the characteristics of the litter to anyone who is acquainted with a beech-maple forest. Even here, however, a classification grouping together the various litters of a common structural type would greatly facilitate comparison of community organization and distributional patterns of the forest floor fauna among different forest types.

The present paper presents a classification of forest floor litter. Although only five forest types from two major geographical areas were studied in arriving at the system, it encompasses a wide range of litter types and is believed to have rather broad application. This is particularly evident when it is noted that many of the characteristics of leaves from Montane Rain Forest appear to be similar to those

from the Rain Forest formation described by Richards (1952). However, it must be emphasized that this classification is not considered complete but simply a nucleus of exemplary types to which many more will undoubtedly be added by future workers as the need arises.

In studying forest floor organisms, it is important to understand the structure of their habitat, the changes it undergoes, and the distribution of litter and humus in the forest floor. Few comparisons of these properties have been made among even relatively well studied temperate forest types and comparisons between temperate and tropical areas are almost completely lacking. Indeed, the characteristics of the forest floor in most tropical formations have not been adequately described. For these reasons a rather detailed analysis of the forest floor has been made in selected communities from both temperate and tropical areas, and its properties expressed in quantitative terms which permit direct comparisons.

The forest floor is considered to be "the whole of the organic material on the soil surface (including litter)," as defined by the Third International Congress of Soil Science in Oxford (Heiberg 1937). The stratification of the forest floor into morphologically distinct layers was early discovered and several nomenclatural systems for it have emerged. Three major layers are recognized: an uppermost stratum of relatively unaltered plant and animal remains, a middle one consisting of fragmented and partly decomposed products derived from the top layer, and a

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bottom one of amorphous, finely divided organic matter, the origin of which, in contrast to the material of the previous two strata, is unrecognizable. Fernow *et al.* (1917), in an attempt to systematize forestry nomenclature, called these three strata litter, duff, and humus respectively. With the exception of duff, their terms will be employed in this treatise. Also used because of its convenience is the nomenclature of Hesselman (1925) in which the middle layer is called Förmultningsskiktet (abbreviated to F layer), and the bottom one Humusämneskiktet (abbreviated to H layer). His term for litter was Förne and it appears in some European literature represented by the symbol F_0 (e.g. van der Drift 1951) whereas American workers have used the term L layer in its place (Lutz & Chandler 1955). The abbreviated forms, L, F, and H layers will be employed here. Relating these systems to the soil profile, litter or L layer is synonymous with the A_{00} horizon, whereas the F layer and the H layer together make up the A_0 horizon (Lyon & Buckman 1943). In mulls and in the A_1 horizon of soils in which organic matter is mixed with mineral soil, the term H layer is not considered as applicable to the mixture.

The aid of the following individuals and institutions is gratefully acknowledged: F. H. Test, Department of Zoology, University of Michigan, who supervised the research and provided valuable suggestions and criticism; S. H. Spurr, C. F. Walker, and W. R. Murchie, for council and advice; A. H. Stockard, Director of the University of Michigan Biological Station, for permission to use the facilities of the Station; Dirección Recursos Naturales Renovables of the Venezuelan Ministerio de Agricultura y Cria, especially Srs. Herman Martinez Salas, Ricardo Gondelles Amengual, and Francisco Tamayo for providing transportation and lodging during my stay in Venezuela; Sr. Walter Arp, Director of Estación Biológica Henry Pittier, for making research facilities available; Srs. Baldur Terzenbach and Pablo Carmone, and Miss Marilyn Davidson, for assistance in the field; A. R. Test and O. J. Sexton, for many suggestions and aids which facilitated my work; H. Deditch, J. W. Burnham, and F. J. Parker, and the Argus Camera Company, for permission to use their properties as study areas; W. S. Benninghoff, for permission to use data obtained by his class in plant ecology; S. B. Preston, for identifying wood samples; Srs. L. Aristeguieta and T. Lasser, for plant identifications; L. Hill, for aid with soil analyses; and my wife, Audry, for helping to prepare the figures, typing the manuscript, and assisting in the field. This work was supported by grants from the National Science Foundation and the Horace H. Rackham School of Graduate Studies, University of Michigan.

STUDY AREAS

Three general areas were used for this investigation: north central Venezuela, northern Michigan, and southern Michigan. The forest types involved

were Montane Rain Forest in Venezuela, oak-hickory forest and swamp hardwoods in southern Michigan, and beech-maple and oak-pine-aspen communities in northern Michigan.

Most of the forest types used are widespread in their respective geographical regions, although swamp hardwoods usually occupy less extensive tracts than the others. Montane Rain Forest is commonly found on mountains in the tropics.

Studies were carried out in the Montane Rain Forest from late June to early September, 1956, in northern Michigan from late June to mid-August, 1957 and 1958, and in southern Michigan from late March to early June, 1957 and 1958, as well as October, 1957.

BEECH-MAPLE FOREST

This study area was in Emmet Co., Michigan, on the western edge of the village of Carp Lake (Carp Lake Township, T.38N., R.4W., S.10).

The terrain was generally level, but there were occasional small depressions and mounds on the forest floor subsequently referred to as microtopographical features.

The well drained soils in the northern Lower Peninsula of Michigan are podzols. The one occurring at the Carp Lake study area belongs to the Kalkaska-Mancelona-Rubicon Association (Veatch 1953) and is either Kalkaska sand or loamy sand, although no detailed soil map was available and a pedological analysis was not made. The humus was granular mor.

A single soil pit showed an A_1 horizon 5 cm thick, a gray A_2 horizon of 14 cm, and a rust colored B horizon going down 13 cm more, at which point a dark brown ortstein was encountered.

Readings of pH taken with a Beckman pH meter were 5.95 for the F layer, 4.95 for the H layer, and 4.95, 4.85, and 4.85 in the A_1 , A_2 , and B horizons respectively. A crushed sample of the underlying ortstein gave a reading of 5. The surprisingly low pH values can probably be attributed to the presence of hemlock in the community.

The owners said there had been no fire in the forest during the 30 years of their residence and probably not for a much longer time. The same statement applies to logging for one part of the forest, although individual windthrown trees had been taken out occasionally. In another part, however, a rather large number of trees had been windthrown and were removed about 1940, allowing a dense growth of saplings to develop. A third part had been disturbed in some manner at a still earlier time, as species belonging to successional stages as well as to the beech-maple climax were present. These three parts of the forest will subsequently be called the mature section, sapling section, and second-growth section, respectively.

The large trees in the mature and sapling section were beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and lesser numbers of hemlock (*Tsuga*

canadensis). The saplings in the latter area were mostly red maple (*Acer rubrum*). Differences in ground-vegetation between the three sections were chiefly quantitative. For a more detailed description of the area refer to Heatwole (1959).

OAK-PINE-ASPEN FOREST

The stand in which studies were made is located on the grounds of The University of Michigan Biological Station, in Cheboygan Co., Michigan, between Douglas and Burt lakes (Munro Township, T. 37N., R.3W., S.33). The investigation was restricted to an area just south of the Pellston-Cheboygan road approximately 0.5 mi west of the station's entrance. The study area was on late Pleistocene beaches between the Algonquin and Nipissing levels (Spurr & Zumberge 1956, Spurr 1956).

Small depressions about 0.5 m deep and less than 2.5 m in greatest diameter were scattered throughout the forest. The soil was Roselawn sand (Foster *et al.* 1939). Humus, where present, was of the mor type. In a single soil pit, the A₁ horizon with infiltrated humus was 5 cm thick, the leached gray A₂ horizon 12 cm thick, underlaid by an orange-brown B horizon extending down 58 cm more before becoming paler. Readings of pH, taken with a Beekman pH meter at depths of 2.5 cm, 11 cm, 27 cm, and 75 cm from the soil surface were 4.7, 5.8, 5.6, and 5.8 respectively. In taking soil moisture samples, I noticed that the A₁ horizon was often thinner than the above values, and was often absent under patches of lichens.

Voss (1956), in tracing the history of floristics in Emmet and Cheboygan counties, indicated a period of lumbering beginning in 1844, reaching a peak about 1896, and then gradually declining. Pine was taken first, followed by hardwoods. After lumbering there were fires which also influenced the vegetation. Both of these factors have been important in the oak-pine-aspen study area, although specific dates of fires or cuttings on the site are not available. Numerous flat-topped stumps attest to lumbering activities, and subsequent fires are evidenced by the charred condition of some of them.

At the present time, the stand is very sparse with many large gaps in the canopy.

The dominant trees in the community were *Quercus rubra* var. *borealis*, *Populus grandidentata*, and *Pinus resinosa* with respective importance values of 38.4, 17.7, and 7.7 as determined by a phytosociological analysis carried out by the plant ecology class at the biological station in July, 1957. Thirteen plots were used, each 20 m x 20 m. Other tree species present but with lower importance values were *Acer rubrum* (4.3), *Pinus strobus* (0.4), and *Pinus banksiana* (6.2).

The ground layer was very heterogeneous. Large clones of *Pteridium aquilinum* var. *latiusculum* were abundant throughout the community, this species having the highest importance value of any herbaceous plant (32.3). Other plants also formed discrete vegetational units, the most important ones being

Vaccinium vacillans (5.8), *Vaccinium angustifolium* (2.3), *Gaylussacia baccata* (2.0), and *Poa compressa* (5.8). The only additional vascular plant with an importance value greater than 1.0 was *Carex pennsylvanicus* (2.4). Minor herbaceous species commonly seen in the immediate study area were *Hieracium aurantiacum*, *Hieracium florentinum*, *Hieracium venosum*, *Senecio pauperculus*, *Solidago* sp., *Aster* sp., *Antennaria* sp., *Krigia virginica*, *Melampyrum lineare*, *Silene antirrhina*, *Rumex acetosella*, *Gaultheria procumbens*, *Verbascum thapsus*, *Pyrola virens*, and *Monotropa hypopithys*, as well as occasional individuals of other species. The moss *Polytrichum juniperinum* was present and the lichens, *Cladonia rangiferina*, *Cladonia mitis*, *Cladonia uncialis*, and *Cladonia alpestris* formed large patches on the forest floor. The net effect was a mosaic formed from clones of different herbaceous or shrubby species, interspersed with patches of fruticose lichens and bare areas. Again, reference can be made to a more detailed description of this area given by Heatwole (*op. cit.*).

OAK-HICKORY FOREST

This area was located in Washtenaw Co., Michigan (Webster Township, T.15, R.5E., S.1) just southwest of Mud Lake.

Dominant trees were *Quercus alba*, *Quercus velutina*, and *Carya ovata*. Shrubs were present in patches and the herbaceous cover was varied, containing grasses in addition to other ground-layer plants common in Michigan forests of this type. A small woodland pond was present which contained standing water at least during spring and early summer.

The soil was Miami loam (Veatch *et al.* 1930) with a mull type of humus. The pH of a single surface sample was 6.

SWAMP HARDWOOD FOREST

This study area was located in Washtenaw Co., Michigan (Webster Township, T.1S., R.5E., S.1) just north of Mud Lake. The property belongs to the University of Michigan and has been set aside for research since 1957. Graham & Hunt (1958) have published a map of the area.

The Mud Lake region is characterized by gently rolling hills with the lowlands between them occupied by marsh, bog, or swamp resulting from filling in of a morainal lake following the Wisconsin glaciation. The upland just north of the swamp hardwoods represents the terminal moraine of the Huron-Erie ice lobe, whereas the smaller areas (e.g. the oak-hickory area previously described) are kames and deposits of ground moraine (Russell & Leverett 1915).

The swamp itself was relatively flat in gross features. However, around trees and the proximal part of their root systems, mounds had developed which were higher than the general level of the forest floor. In addition there were depressions which were

filled with water during the spring and early summer, forming numerous pools.

The substrate in the swamp hardwood study area was Rife peat (Veatch *et al.* 1930), a black, mucky soil consisting chiefly of organic material. Readings of pH from two surface samples, one each from the northern and southern parts of the swamp were 5.2 and 4.8. The southern edge of the hardwood swamp where the lower value was obtained borders a bog mat.

The dominant species were *Ulmus americana*, *Acer rubrum*, and *Betula lutea*. The canopy was relatively open. The shrub layer was not well developed although *Rhus vernix* and occasionally other species were present. The herbaceous layer consisted chiefly of the ferns, *Osmunda regalis*, *Osmunda cinnamomea*, *Onoclea sensibilis*, and *Dryopteris spinulosa*, skunk cabbage (*Symplocarpus foetidus*), and mosses. Additional ground-layer species, at least in some parts of the swamp, were *Caltha palustris*, *Coptis groenlandica*, *Trientalis borealis*, *Maianthemum canadense*, *Boehmeria cylindrica*, *Impatiens capensis*, and *Vaccinium angustifolium*. In places the herb cover was quite dense and by late summer was waist high. Refer to Heatwole (*op. cit.*) for further descriptive details.

MONTANE RAIN FOREST

This research area was located near the Estación Biológica Henry Pittier in north central Venezuela between Lake Valencia and the Caribbean Sea, 7 km northwest of the city of Maracay (21.5 km by road). The biological station is part of the Parque Nacional Rancho Grande in the state of Aragua, and has itself been formerly known as Rancho Grande. It is close to Portachuelo Pass in the Cordillera de la Costa mountain range and lies at an altitude of 1095 m above sea level. Slopes are steep, the range of 20 values taken with a pocket transit at 15 m intervals along a transect line was 11°-43° from the horizontal. The soil is a yellow clay loam with red patches locally.

The station is situated in a formation variously called Cloud Forest by Beebe & Crane (1947) and Montane Rain Forest by Beard (1944, 1955). The latter name will be used here. It contains two closed tree stories at roughly 10 m and 20 m and rather sparse herbaceous and shrubby undergrowth except where mature trees have fallen and produced an opening. Tree ferns are common, as are palms, including dwarf species and those with stilt roots; lianas and vines are occasional, whereas epiphytes are extremely abundant (chiefly bromeliads, ferns, orchids, and bryophytes). The older tree leaves support growths of epiphyllae. The forest as a whole is evergreen although some species shed their leaves during the dry season. Such features as cauliflory, tree buttresses, red color of new leaves, and presence of drip tips which are common in several tropical forest types (Richards 1952) are also present in this montane formation.

Pittier (1939) in writing of the "selva nublada" or Montane Rain Forest in the Rancho Grande region,

gave *Gynertheria caribensis* as the dominant tree. The following he lists as frequent: *Brosimum utile*, *Spondias lutea*, *Inga marginata*, *Fagara ocumarensis*, *Abarema trapezifolia*, *Coussapoa villosa*, *Hedyosmum bouplandianum*. A spiny palm is also quite abundant which Beebe & Crane (1947) called *Bactris* sp. and considered an immigrant from a neighboring zone. In the present investigation only species which were in flower during the study period were collected. The only additional tree species identified was *Eschweilera cf. perumbonata*. Smaller plants identified were *Solanum ombrophilum*, *Schonenobiblos daphnoides*, *Chrysochlamys membranacea*, *Cestrum* sp., and *Anthurium cf. bredemeyeri*. Ferns are abundant and include epiphytes and climbing species as well as terrestrial forms. Species identified were *Asplenium radicans*, *Danaea alata*, *Danaea elliptica*, *Polytaenium cayaennense*, *Hemithelia karsteniana*, and *Davalliopsis elegans*. Along the sides of streams and rock slides or under openings in the canopy, araceous plants such as *Dieffenbachia* sp. and *Heliconia* sp. were encountered as well as many other herbaceous ones; those identified were *Diastemma longiflorum*, *Phytolaca* sp., and the grass *Pariana* sp. The principal second-growth tree was *Cecropia* sp. Unfortunately many important species could not be identified and perhaps some of those included here are very minor elements.

Temperatures are relatively uniform and rainfall is high. Fog is of daily occurrence. General characteristics of this area are also given by Schäfer & Phelps (1954), Mertens (1957), and Heatwole (1959).

NOMENCLATURE AND CRITERIA USED IN CLASSIFICATION OF LITTER TYPES

The system of classification comprises three large categories termed classes, each containing a number of sub-units called types. In defining these, characteristics were used which are easily recognizable in the field, are relatively stable under the range of conditions ordinarily found in the forest type concerned, and are potentially important to the resident fauna. Classes are based on the structure of the stratum, types on the form, size, or habit of the majority of component objects. A more detailed treatment of the less easily observed features is reserved for the section on analysis of the forest floor habitat.

Variation in moisture conditions may influence litter structure to some degree and the criteria set forth here should be used under the usual range of conditions in the forest in question and not applied to litter moved from its normal site. Extreme drying or wetting tends to cause curling or flattening of some leaves and moisture differences between stands of the same forest type in separate localities may conceivably result in different litter structure. Also seasonal changes in litter structure corresponding to moisture conditions may occasionally occur. However, the effect is not of sufficient magnitude to impair the usefulness of the classification.

Choice of names for classes and types was guided by the dual goals of brevity and descriptive value. Each class was assigned a Roman numeral whereas each type was given a name in the form of a descriptive adjective indicating one of its distinctive features. Unless the class to which a type belongs is clear from context, the type name is preceded by the Roman numeral of the class. The initial letter of the adjectival part of the name of each is capitalized. Table 1 presents keys for distinguishing the classes and types thus far recognized.

TABLE 1. Key to classes and types of litter.

A. Key to classes	
1. Composed chiefly of broad leaves or needles, often forming a continuous carpet on the forest floor.....	2
1 ¹ . Composed chiefly of woody objects not forming a continuous carpet on the forest floor.....	Class III
2. Leaves lying flat upon each other, interstitial spaces small.....	Class II
2 ¹ . Leaves curled or sharply bent, interstitial spaces large.....	Class I
B. Key to types of class I	
1. Most of the leaves large with many tough but flexible leaflets, forms brushy heaps often discontinuously distributed on the forest floor.....	Complex
1 ¹ . Most of the leaves not as above.....	2
2. Most of the leaves bent at the midrib, forming a V in cross section.....	Bent
2 ¹ . Most of the leaves curled or rolled.....	Curled
C. Key to types of class II	
1. Most of the leaves broad.....	2
1 ¹ . Most of the leaves needle-like.....	Needle
2. Most of the leaves thick and leathery.....	Thick
2 ¹ . Most of the leaves thin and papery.....	Thin
D. Key to types of class III	
1. Objects less than 10 cm in diameter.....	Small
1 ¹ . Objects 10 cm in diameter or greater.....	2
2. Objects firm, solid and undecayed.....	Solid
2 ¹ . Objects not firm and solid, and at least partly decayed.....	3
3. Objects composed of blocks or chunks with cracks between them.....	Chunky
3 ¹ . Objects not composed of chunks or blocks.....	4
4. Objects composed of soft partly decayed wood fibers.....	Fibrous
4 ¹ . Objects composed of finely divided particles.....	Crumbly

Although there are some difficulties encountered in application of this (as any) system of classification, I have found it to be quite useful and believe that it is adaptable to many situations.

DESCRIPTION OF CLASSES AND TYPES OF LITTER

CLASS I

The chief feature delimiting this class is the habit of the leaves, which may be curled, bent, or otherwise contorted, thus forming large interstitial spaces and imparting a loose structure to the litter layer.

The class is widely distributed, being found as a major form under several forest types in the North Temperate Zone as well as in Venezuelan Montane Rain Forest.

(1) Type I Bent. The leaves of which this type is chiefly composed, bend at the midrib to form a V when viewed in transverse section (Fig. 1). As they tend to maintain this shape against mechanical pres-

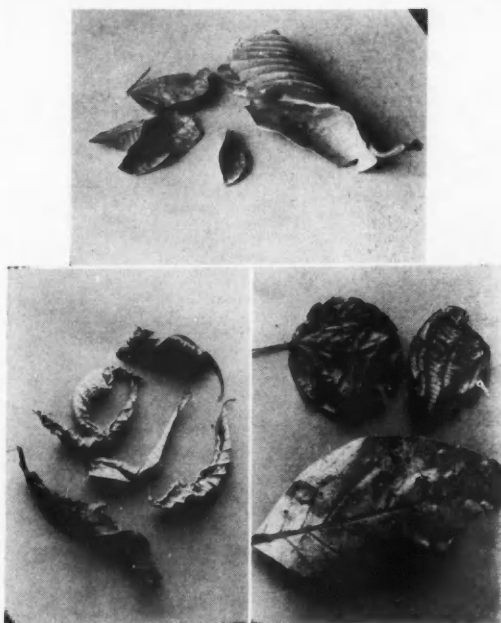


FIG. 1. Leaves from Montane Rain Forest. Top: typical leaves constituting type I Bent litter. Lower left: typical leaves constituting type I Curled litter. Lower right: typical leaves constituting type II Thick litter.

sure and do not compact easily, a very loose, yet stable litter results with large interstices between the leaves. Usually the leaves are highly cutinized and have a prominent midrib and lateral veins which make them tough and rigid. Leaves of *Gynerthera caribensis* as well as many unidentified Montane Rain Forest species had this form. The leaves making up this type were usually simple with entire margins although one bipeltate kind also occurred.

This type was also found in Venezuelan Deciduous Seasonal Forest, an altitudinally lower vegetational belt bordering Montane Rain Forest. It was not present in Michigan forests.

(2) Type I Curled. This type is characterized by thin leaves of papery consistency which tend to curl or roll up after abscission. The resulting litter is less resistant to mechanical pressures than the previous one. Both share the characteristic of large interstices. However, in this type the interstices have rounded outlines whereas they are angular in I Bent. Many kinds of leaves form this type of litter, e.g., oak, elm, and unidentified Montane Rain Forest species (Fig. 1).

In the present study this type was present in the Montane Rain Forest and also in oak-pine-aspen woodland at The University of Michigan Biological Station where it was composed chiefly of oak and aspen leaves (Fig. 2).

(3) Type I Complex. This type is made up



FIG. 2. Typical type I Curled litter from the oak-pine-aspen area containing leaves of *Quercus rubra* var. *borealis* and *Populus grandidentata*. Note tendency of the oak leaves to curl or roll and of the aspen leaves to curl at the edge.

chiefly of large palm leaves. The pinnae are tough but flexible. When these massive leaves fall to the forest floor the pinnae form a complex structure with large interconnecting interstices having angular outlines. Although a discontinuous distribution on the forest floor is characteristic, aggregations of a number of leaves commonly occur.

In the present study this type was found only in Venezuelan Montane Rain Forest. It is probably confined to tropical and sub-tropical areas.

CLASS II

This class is distinguished by the way in which the leaves lie relatively flat, one upon the other, thus forming interstitial spaces which are small. It was frequently encountered in Michigan and was also a common class in Venezuelan Montane Rain Forest.

(1) Type II Thick. This type is composed of tough, leathery leaves, which do not curl or bend but maintain their flattened configuration. They tend to form a layered or laminated structure with relatively small, flat interstices (Fig. 1). The leaves forming



FIG. 3. Typical type II Thin litter from the beech-maple study area containing leaves of *Fagus grandifolia* and *Acer rubrum*. Note flat habit of the leaves.

this kind of litter are usually large and broad, and have entire margins.

In the present study it was encountered only in Venezuelan Montane Rain Forest.

(2) Type II Thin. The feature distinguishing this type from others of the class is the thin, papery consistency of the component leaves. This makes the litter less resistant to mechanical forces than II Thick. Comparison of decay in these two types will be discussed later. The L layer is a somewhat laminated structure because of the absence of pronounced curling or bending of the leaves (Fig. 3). The component leaves have various shapes. The interstices are small and flat as in the previous type.

This occurred in beech-maple forest but was not found in Venezuelan Montane Rain Forest.

(3) Type II Needle. This type consists of the various conifer litters formed from needles lying closely together and forming a compact layer with small angular interstices (Fig. 4). Indeed, this type often appears to be more compact than most broad leaf ones. It is so distinctive that it hardly needs a description for anyone familiar with temperate or boreal forests. However, it is an exceedingly rare type in tropical areas, and was lacking in Venezuelan Montane Rain Forest. This type and type I Complex



FIG. 4. Typical type II Needle litter from the oak-pine-aspen study area containing needles of *Pinus resinosa* and scattered oak leaves.

are the only ones which can be correlated with the taxonomic position of contributing trees.

CLASS III

This class consists of litter types composed chiefly of woody objects. Unlike the other classes, it is almost always distributed discontinuously as relatively small, discrete units. It is probably present in every forest unless its accumulation is prevented by man.

(1) Type III Small. This type is composed chiefly of woody objects less than 10 cm in diameter. It may not naturally occur but is sometimes found where man has piled up twigs and small branches to form a brush pile. Small sticks, nuts, and other similar objects when occurring as scattered or isolated items over the forest floor are here treated as part of the litter type in or on which they are found. Similarly, isolated leaves which would tend to form a different type of litter than the one in which they are found are considered as part of the type in which they occur. Thus it is the overall structure of the litter which is important.

(2) Type III Solid. This type, and the following two as well, are composed of logs (woody objects 10 cm or greater in diameter). These objects are so large that they create a completely different structural unit from the rest of the litter which surrounds them, and hence I have set them aside as distinct types. Type III Solid includes those logs which are newly fallen, still retain their bark, and are undecayed. The only spaces within the structure itself are tree-holes or tunnels bored by insects.

(3) Type III Chunky. This type consists of logs which are in the initial stages of decay and have broken down into chunks of wood 2-10 cm wide by 5-15 cm long. Each chunk is firm but is separated from its neighbor by a crack or plane of separation which provides space for occupancy by organisms (Fig. 5). In the present study this kind of structure occurred in old hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*) logs.

(4) Type III Fibrous. This type is made up of logs which in the process of decay have become

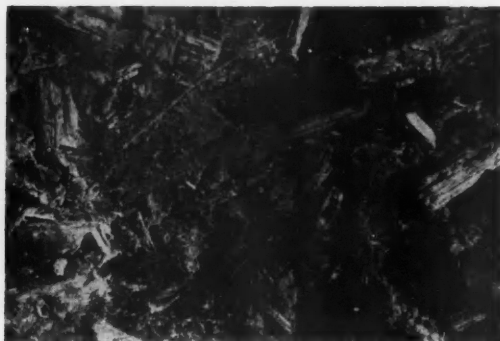


FIG. 5. Typical structure of type III Chunky litter as exposed in an opened log.

softened but not separated into discrete chunks. The wood occurs in loosely connected strands or fibers. There are very few cavities in this type except those made by insects. The type is composed chiefly of deciduous species although some white pine logs also had this internal structure.

(5) Type III Crumbly. This type contains logs in a rather advanced stage of decay. The wood can be crumbled in the hand. It is broken down and is present as finely divided particles (Fig. 6). There



FIG. 6. Typical structure of type III Crumbly litter as exposed in an opened log. Note clutch of salamander eggs in center of picture.

are no large spaces within the logs but because of the structure they are probably usable by many burrowing forms. Both deciduous and conifer species fall in this category.

LEAF THICKNESS

One of the criteria used in classifying different kinds of litters was whether component leaves were "thick" or "thin." These words have relative meanings and are significant only when some indication of limits is given. For this reason, leaves from the different litter types were measured in order to more precisely define the usage of "thick" and "thin" in the scheme of classification.

Samples of newly fallen dry leaves collected in November from the northern Michigan study areas

were measured in the laboratory with a micrometer. Dry Montane Rain Forest leaves were also measured but these had been stored in boxes from 1956 to 1958. All measurements were to the nearest five-thousandths of a millimeter, at a position on the leaf midway between the base and apex of the blade and halfway between the midrib and outer margin. Care was exercised in avoiding large veins and wrinkles. The samples from Michigan were sorted into species and 50 leaves of each species measured. Samples of Montane Rain Forest types available at the time of measuring were small and all leaves were measured without sorting into taxonomic categories. This in part accounts for the greater ranges in leaf thickness for Montane Rain Forest types.

Two definite groups resulted (Table 2). One contained leaves from the temperate areas and type I Curled from Montane Rain Forest (mean thickness less than 0.20 mm), the other included types I Bent and II Thick (mean thickness greater than 0.20 mm). These figures are not set as standards for identifying the type to which a particular litter belongs but do show quantitatively the differences which exist between types subjectively grouped as "thick" or "thin." Type II Thick had a mean leaf thickness of 0.271 mm whereas the maple and beech leaves making up type II Thin had corresponding values of 0.086 mm and 0.092 mm respectively.

TABLE 2. Mean thickness of leaves from various litter types. University of Michigan Biological Station is designated by U.M.B.S.

Litter type or species of leaves	Locality	N	Mean leaf thickness and 95% confidence limits (mm)	Range in leaf thickness (mm)
<i>Acer saccharum</i>	Carp Lake	50	.086 ± .004	.070-.115
<i>Fagus grandifolia</i>	Carp Lake	50	.092 ± .005	.080-.235
<i>Populus grandidentata</i>	U.M.B.S.	50	.120 ± .006	.095-.170
<i>Quercus rubra</i> var. <i>borealis</i>	Mud Lake & U.M.B.S.	50	.140 ± .008	.100-.200
I Curled.....	Venezuela	27	.154 ± .016	.095-.250
I Bent.....	Venezuela	50	.304 ± .018	.165-.560
II Thick.....	Venezuela	32	.271 ± .023	.150-.470

It is difficult to evaluate the influence of leaf thickness on the structure of the litter, for factors like degree of cutinization, type and strength of veins, and leaf shape also determine the form a leaf will take after dying and drying out. However, in general it seems that the thick sclerous leaves tend to be flat or bent into a definite shape rather than becoming curled or rolled. Curling or rolling occurs in the thinner ones. Type I Curled is the only type in Montane Rain Forest which contained curled or rolled leaves and in contrast with the other litter from there had leaf thicknesses quite close to those of temperate forests. However, not all thin leaves tend to curl or roll. Beech leaves, for example, have prominent lateral veins which probably aid in maintaining the flat habit of the blade. In addition, maple

leaves, which were the thinnest ones measured, lie flat under the mesic conditions of the beech-maple forest. Effect of moisture on curling has been previously mentioned.

DISTRIBUTIONAL PATTERN

It is generally true of temperate regions that the forest floor contains a rather uniform and continuous layer of a single leaf litter type, although an exception was noted in the oak-pine-aspen forest of the present study. This was not true of the Venezuelan study area, and the presence of bare soil was one of the striking features associated with Montane Rain Forest. Here, several litter types were present and tended to form a mosaic pattern in which patches of exposed soil were interspersed.

In order to find the relative area occupied by exposed soil and different litter types in the beech-maple forest, stakes were placed at 10 m intervals along a transect line running northeast to southwest. A cord 2 m long was stretched from each stake in a northwest direction over the various litter types and the lengths of the cord intercepted by each of the types, bare humus, or bare soil was measured. Of the resulting 70 line-intercepts, 41 were in mature forest, 22 in the sapling section and 7 in the second-growth. Relative area of the most abundant type (II Thin) was between 92 and 96% in the three sections (Table 3). Thus all three sections are quite similar and can be grouped for further analysis.

TABLE 3. Per cent of forest floor covered by the various litter types in beech-maple forest, Carp Lake, Michigan.

	II Thin	II Needle	III Small	Logs	Exposed Humus
Mature section....	93.0	1.0	4.9	0.7	0.3
Sapling section....	92.1	3.7	4.0	0.1	0.1
Second-growth....	95.4	0	3.9	0.8	0

In the oak-pine-aspen study area, a line transect 100 m long was marked out from north to south and used as a single line-intercept. However, the accuracy of measurement was only to the nearest 10 cm. Thus, these data are of a more general nature than those from the preceding areas and from Montane Rain Forest.

A slightly different technique was used in Montane Rain Forest, although the data are comparable. Two transect lines, each 230 m long, were marked out in the Portachuelo Pass study area with the aid of a pocket transit. One transect ran north and south, intersecting the second at right angles, the point of intersection being at the center of both lines. Sample plots one meter square were outlined at the center point and at 16 m intervals along each segment of the transects, making a total sampling area of 41 m². The central plot was located on the top of a ridge

with the segments of the transect including both horizontal and steeply inclining topography. Sample plots were mapped to scale according to litter types, sticks, plants, stones, roots, and exposed soil, F layer or H layer, and then the relative area of each obtained.

A sharp contrast is seen in the proportion of exposed soil devoid of organic material in the three forests. Both temperate forests lacked such places except on a few mounds which did not occur in the samples, whereas Montane Rain Forest had 19.8% of the total area bare (Fig. 7). This may be a rather common feature of tropical forests, as Richards

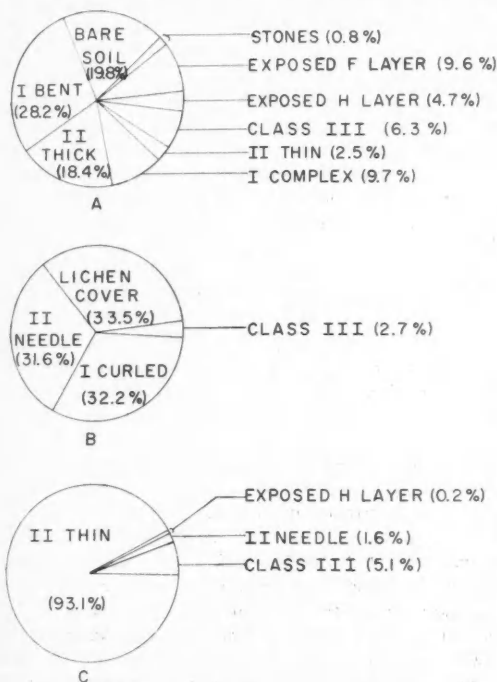


FIG. 7. Relative area occupied by the different litter types, bare soil, and exposed F and H layers. A. Montane Rain Forest, B. Oak-pine-aspen forest, C. Beech-maple forest.

(1952) states that patches of bare soil are often found in the Rain Forest formation. Evidence that the great amount of bare soil is not due to a single large denuded area along some part of the transect is found in the high frequency of occurrence (80.5%) of exposed earth in the sample plots.

Montane Rain Forest contained many places in which the F or H layer was uncovered whereas this seldom occurred in temperate forests. Bare humus and fragmented leaves accounted for less than one per cent of the area in the beech-maple forest but makes up 14.3% of the floor of the Montane Rain Forest. These sites may represent former litter patches in an advanced state of decomposition, or perhaps are

portions of the forest floor which, due to greater stability, remain after water action has removed the L layer.

In order to look further at the abundance of types which do not have high cover values in Montane Rain Forest, counts of the number of fallen palm leaves (type I Complex) and dead stumps and logs were made while walking along the transect. All pertinent objects of which a part fell within 3 m of either side of the transect were included (total area equals 578 m²). There were 260 palm leaves not counting those of dwarf palms, 29 stumps, and 100 logs. Neither actual abundance nor relative coverage of stumps or logs can be compared among the forest types because, except for Montane Rain Forest, the number of these objects on the forest floor has been affected by man's activities. Therefore distribution of this type as measured for the temperate areas cannot be considered a true property of the forest.

Another comparison which can be made is the number of litter types represented in a forest community. A single litter type predominates almost to the exclusion of others in the beech-maple forest.

The mosaic distribution of litter in the oak-pine-aspen area is probably a somewhat aberrant situation for temperate forests and results in two litter types of high coverage values. However, the stand was quite open and type II Needle accumulations were restricted to the vicinity of pine trees, whereas I Curled occurred anywhere in the forest where there were depressions or a cover of ground vegetation. Accumulations of the latter type is probably prevented elsewhere by wind action. A denser stand of the same species might not display such a mosaic pattern.

The Montane Rain Forest contained three litter types of high coverage value as well as several others of minor importance. Two of the three types with large cover values, I Bent and II Thick, were represented in a very high frequency of plots (82.9 and 78.0% respectively). The third major type, I Complex, was present in almost half of them (46.3%). Therefore these types were distributed throughout the transects and were not clumped in any one small section. Forty-two per cent of the plots in Montane Rain Forest contained two litter types and 36% contained three. The percentage of plots with four types or only one type was rather small (10% and 13% respectively). When the size of the plots (1 m²) is considered, the extreme dissection of the L layer into small patches of different types is evident.

The patchy distribution of litter types in the temperate oak-pine-aspen stand was quite different than in Montane Rain Forest in that accumulations of a given litter type were generally much larger. Along the line-intercept through oak-pine-aspen, the smallest length of cord intercepted by II Needle was 0.8 m, and 0.3 m for I Curled. Maximum values obtained along the transect were 11.4 m and 5.0 m

respectively, although larger ones were present elsewhere in the area.

THICKNESS OF THE FOREST FLOOR STRATA

Two of the chief factors involved in determining the size of the litter habitat are distribution and depth of the L layer. The former has been discussed above. Depth will now be considered. Litter depths were obtained by taking a total of 120 measurements in the sample plots located along the transects in the Montane Rain Forest (1-6 measurements per plot depending on amount of bare area). In the other study areas, measurements were made along a straight line at 5-m intervals, omitting those points not falling on the type of litter being measured. In every instance zero values were not included in the calculations. Thus the data represent average depth of each litter type where it occurred, not the average depth if spread over the entire forest floor. Because of the effects of microtopography on depth, considered later, measurements taken in depressions or on mounds have been excluded from the calculation of means and ranges. Measurements were taken in summer or early autumn before leaf fall had occurred.

Mean, range, and twice the standard error were plotted (Fig. 8) for each type of leaf litter. There was no sharp break between depth of class I and class II although the former tended to occur in deeper accumulations. Some of the reasons for this will be discussed later. The L layer in the swamp hardwoods was shallow as compared to other areas with the same class. This may be accounted for by the wet conditions of the muck which would facilitate rapid

decay of the bottom leaves thereby bringing those from further up in the stratum into contact with the substrate. Type II Needle litter showed the least depth of any type. This corresponds to observations on coniferous forests in general.

The values of N for type I Complex and I Curled from Montane Rain Forest were too low for the samples to be considered adequate. Nevertheless the extreme depth encountered in the former (60 cm) gives an idea of the large loose structures made by palm fronds on the forest floor. The great range in depth of I Bent is attributed to the large number of different species of leaves in the Montane Rain Forest. At some sites occupied by I Bent litter there were scattered leaves which were flat or curled and which had an influence on litter structure. This will be discussed later in more detail. As evidenced by the larger standard errors, class I litters showed greater variation in depth than the class II ones. This is probably because compact litters have very little space and therefore mechanical disturbance (animals, falling rain) do not alter the structure as much as they do in the looser types. It should be pointed out that the large standard errors of I Curled and I Complex litters from Montane Rain Forest are large because of the smallness of the samples and not necessarily because of great variation in depth.

Another interesting point is that litter in the oak-pine-aspen area was almost as deep on the average as in the oak-hickory area (4.6 cm and 5.1 cm respectively). This occurred despite the much denser canopy in the oak-hickory forest. However, it may be remembered that litter tends to accumulate around ground vegetation in the oak-pine-aspen area and is not evenly distributed over the forest floor. Inasmuch as zero values were not included in calculations of mean litter depth, the similarity in the two areas was not surprising. The effect of ground-vegetation on litter structure may also be a factor and is discussed later. In the beech-maple forest where there was a continuous litter cover (no zero values) the depth was significantly greater in the mature than in the sapling and second-growth section. The sapling section had greater depths than second-growth. Here the difference may have resulted from decrease in number of trees contributing leaves in the sequence mature-sapling-second growth.

Average depth of the F layer was obtained in the same manner and under the same conditions as that of the L layer. At points where an F layer was present it was on the average deeper in beech-maple than in Montane Rain Forest (Fig. 9). This relationship did not hold for the humus layer and no significant difference between mean depths of humus accumulations in the two forest types was indicated.

In considering the above data, as well as those for the L layer, it must be remembered that the depths were taken where the given substrate was present, i.e. all zero values were omitted. Calculation of the total amount of fragmented material and humus on the forest floor would also have to take distribution into

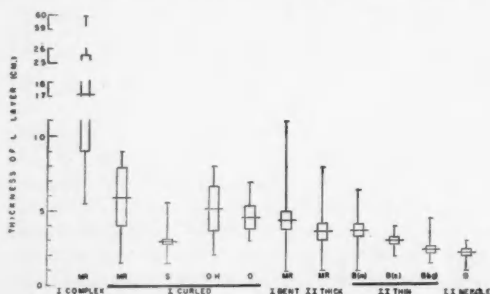


FIG. 8. Depth of litter in the study areas. Vertical line represents range, horizontal line the mean, and the rectangle twice the standard error on each side of the mean. Depths taken in Montane Rain Forest in July 1956, in the temperate forest types during summer and early autumn, 1958, before leaf fall had occurred.

B (m)—Beech-maple forest, mature section

B (s)—Beech-maple forest, sapling section

B (sg)—Beech-maple forest, second-growth section

MR—Montane Rain Forest

O—Oak-pine-aspen forest

OH—Oak-hickory forest

S—Swamp hardwoods

N = 65 for I Bent, 40 for I Curled in Swamp hardwoods, 13 for I Complex, 8 for I Curled in Montane Rain Forest, and 35 for all others.

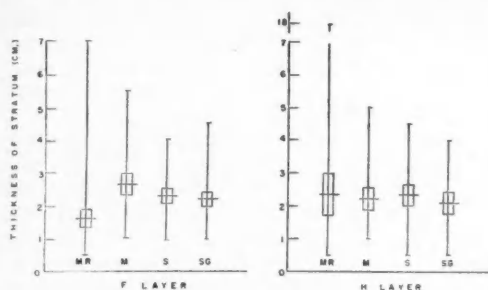


FIG. 9. Thickness of F and H layers. Vertical line represents range, horizontal line the mean, and the rectangle twice the standard error on each side of the mean. Depths taken in Montane Rain Forest in July 1956, in the temperate forest types during summer and early autumn, 1958. Each mean represents an average of 35 values, except in Montane Rain Forest where 107 measurements were made of the F layer and 91 of the H layer. MR—Montane Rain Forest
M—Beech-maple forest, mature section
S—Beech-maple forest, sapling section
SG—Beech-maple forest, second-growth section

account. Discussion of this aspect is deferred until later.

Neither the F nor the H layer is entirely homogeneous throughout. Differences in the F layer are brought about through progressive decomposition and fragmentation from the upper to the lower limits. Sublayers resulting from stratification of the leaf fall of successive years in temperate forests have been designated by van der Drift (1951) from top to bottom as $F_1, F_2, F_3 \dots F_n$, the subscripts referring to the number of years since leaf fall. F_x includes material of all years which are no longer individually distinct. I have not used this distinction because of the difficulty involved in separating the contribution of different years. However, another source of heterogeneity was observed, namely the presence of a network of small rootlets, subsequently designated as a "root mat," in the F and H layers of temperate deciduous forests. Typically the superficial part of the F layer was devoid of rootlets whereas the lower part contained a heavy root mat extending into the upper portion of the humus. Mean thickness of the root mat was measured as previously described and the percentage of the total thickness of the combined F and H layers occupied by the root mat was calculated. The root mat made up 53-65% of the combined thickness of the F and H layers in the beech-maple forest (Table 4). The sapling section had on the average a thicker root mat (3.09 cm) than other sections (2.70 cm and 2.33 cm for mature and second-growth sections respectively). This agreed with the general impression gained during the investigation. However, the differences were not statistically significant.

In the oak-pine-aspen stand on level ground and under type I Curled litter, the root mat was not as well developed as in the beech-maple forest; it averaged 1.22 cm thick in the former and took up 31.0%

TABLE 4. Thickness of root mat in the three sections of beech-maple forest and in the oak-pine-aspen area. Summer, 1958. $N = 35$ for each mean. All samples were taken on level ground.

Site	Litter type	Mean thickness of root mat (cm)	Range in thickness of root mat (cm)	Percentage of combined F and H layers consisting of root mat	
				Mean	Range
Beech-maple mature section	II Thin	2.70 ± 0.43	0-5.0	57.0 ± 7.4	0-91.0
Beech-maple sapling section	II Thin	3.09 ± 0.40	0-6.0	65.0 ± 7.6	0-100
Beech-maple second-growth	II Thin	2.33 ± 0.39	0-5.5	52.6 ± 5.9	0-84.6
Oak-pine-aspen	I Curled	1.22 ± 0.45	0-4.0	31.0 ± 10.2	0-85.7

of the combined F and H layers. The root mat was completely nonexistent under type II Needle litter and patches of lichens in the oak-pine-aspen community.

EFFECT OF TOPOGRAPHY AND HERBACEOUS VEGETATION ON DEPTH AND DISTRIBUTION OF LITTER

All of the above analyses which were made in Michigan were on the basis of relatively smooth parts of the forest floor. In order to secure data on the effect of microtopography on depth of litter, measurements were taken at all mounds and depressions encountered by walking in a straight line through the forest. In the beech-maple stand there were depressions where the roots of windthrown trees had been pulled from the ground. On decomposition these masses of roots and accompanying soil formed mounds adjacent to the depressions. Mounds had also resulted from humification of large stumps and logs. The oak-pine-aspen forest contained depressions but almost no mounds. Both mounds and depressions were usually 2.5 m in greatest diameter or smaller with a vertical dimension of 0.5 m or less. In contrast with the rest of the forest floor, mounds have a thin L layer (mean 2.3 cm for beech-maple) and depressions a very thick one (mean 6.0 cm and 7.6 cm for beech-maple and oak-pine-aspen respectively, Fig. 10).

The uneven distribution shown above may have resulted from movement of the litter. The depressions sheltered the leaves from wind action and tended to hold those blown in from the level forest floor. The opposite was true for the mounds, which were exposed. In addition, water running down the sides of mounds tended to wash leaves into the depressions which were commonly adjacent.

Another possible explanation is that leaf fall was not uniform over the forest floor. Unfortunately, data to test this postulate were obtained only from the swamp hardwoods. Here there was no statistical difference between mounds, depressions, and level areas without low vegetation in mean depth of newly fallen leaves in the autumn (Fig. 11). However, in

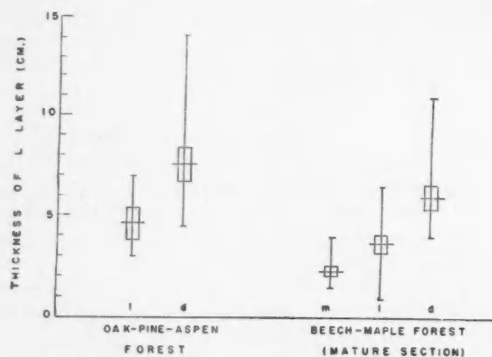


FIG. 10. Effect of microtopography on thickness of litter. Vertical line represents range, horizontal line the mean, and the rectangle twice the standard error on each side of the mean. $N=35$ for each figure. Data collected summer and early autumn, 1958.

m—mounds
l—level microtopography
d—depressions

one of the level areas measured, abundant herbaceous vegetation prevented the dead leaves from settling as compactly as they ordinarily would, and measurements were distinctly greater. Level ground without abundant herbs was not significantly different from other microtopographical types and served as the best comparison, for the depressions and mounds had a similarly slight plant cover at the time of sampling. The effect of vegetation in holding leaves and facilitating litter accumulation has already been mentioned for the oak-pine-aspen area.

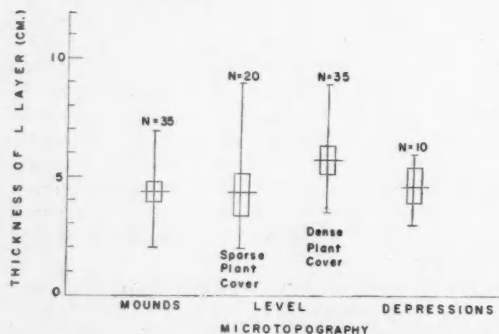


FIG. 11. Effect of microtopography and ground vegetation on the accumulation of newly fallen leaf litter in the swamp hardwood study area, October, 1958. Vertical line represents range, horizontal line the mean, and the rectangle twice the standard error on each side of the mean.

Thickness of root mat in depressions and on level topography were compared in mature beech-maple forest. Depressions contained, on the average, much thicker mats, although the percentage of the combined F and H layers it occupied was not significantly different (Fig. 12). Thus the thicker mats appear

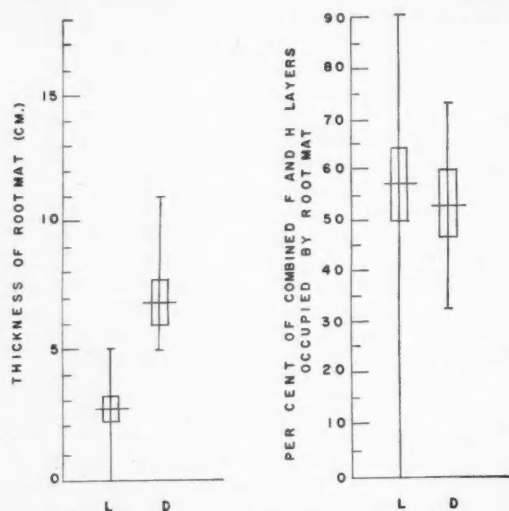


FIG. 12. Thickness of root mat in depressions (D) and on level ground (L) in mature beech-maple forest. Vertical line represents range, horizontal line the mean, and the rectangle twice the standard error on each side of the mean. $N=35$ for level ground and 15 for depressions.

to be related to the greater amount of organic material in depressions. The only three measurements of root mat thickness taken in depressions in the oak-pine-aspen were 5 cm, 4.5 cm, and 6.5 cm, all larger than the thickest one encountered in the 35 samples from level ground in the same litter type (I Curled).

On the basis of a line transect 100 m long in the beech-maple forest it was found that 82% of the forest floor area was level, 11% consisted of mounds and 7% of depressions. Thus the conditions associated with level topography characterized the forest floor generally. Those of depressions and mounds were special local conditions.

TOTAL VOLUME OF HABITAT

It has been shown above that the L, F, and H layers are discontinuously distributed in the Montane Rain Forest and continuous in the temperate forests studied. Microtopography also affected the development of organic strata. In addition, it was shown that where these layers were present in Montane Forest, the H layer was as deep as in beech-maple forest but the F layer not as thick. It was desirable therefore to calculate the average volume of leaf litter, fragments, and humus per square meter of forest floor in order to have some means of comparing the different forests studied on an equal basis which would take into account the variation in depth, distribution and effect of microtopography.

This was accomplished by the formula:

$$V = \left(\sum_{i=1}^n A_n R_n \right) + \left(\sum_{i=1}^n B_n S_n \right) + \left(\sum_{i=1}^n C_n T_n \right)$$

where V equals the mean volume of habitat per square meter of forest floor and A the relative area occupied by a given litter type or organic stratum, on level microtopography. B and C are the same as A except they represent values from mounds and depressions respectively. R , S , and T represent the mean depth of a given litter type or organic stratum (excluding zero values) on level microtopography, mounds, and depressions respectively. The subscript n represents the number of litter types or organic strata involved.

Because of the number of separate data involved, each with some degree of error, the results can only be rough approximations at best. For some forests, lack of separate data on different microtopographical types or elimination of minor litter types contributed additional error. However, certain generalizations can be made.

Oak-hickory had the greatest volume of litter habitat of any of the forests studied with almost twice as much leaf litter as beech-maple forest (Table 5). Montane Rain Forest was next highest. It is not surprising that Montane Rain Forest had a greater mean volume of litter than the oak-pine-aspens as the latter had over one-third of its area covered by lichens, and almost one-third covered by II Needle

TABLE 5. Average volume (cc.) per square meter of forest floor habitat, excluding logs, in selected forest types.

Forest type	L layer	F layer	H layer	Total
Montane Rain Forest	37,000	8,000	4,000	49,000
Oak-hickory	51,000	—	—	—
Oak-pine-aspens	23,000	—	—	—
Beech-maple				
Mature section	34,000	27,000	28,000	89,000
Sapling section	28,000	23,000	24,000	75,000
Second-growth	24,000	22,000	21,000	67,000

litter which was very shallow. However, because of the large area devoid of leaf litter (35%) in Montane Rain Forest it was unexpected that it should have a greater mean volume of litter than beech-maple. This probably occurred because litter in Montane Rain Forest was deeper and contained more space than that in beech-maple, which made up for its less extensive distribution.

A quite different situation was found when mean volume of the F and H layers were compared between forest types. The beech-maple forest had about three times as great a volume of fragmented leaves as Montane Rain Forest, and 5-7 times as much humus. The total volume of forest floor habitat was about one third greater in beech-maple than in Montane Rain Forest.

COMPRESSION CHARACTERISTICS AND INTERSTITIAL SPACE

The extent to which an L layer can be compressed is a measure of the interstitial space. Compression

data were obtained by measuring the thickness of the L layer, placing a standard weight on it, and then remeasuring. Values were expressed in per cent compression, i.e., the difference in depth divided by the initial depth times 100.

In Venezuela a brick exerting a downward force of 0.025 lbs per cm^2 was used as the standard weight. Depth measurements were made by driving a sharp-pointed stick calibrated in centimeters into the ground and noting the position of the bottom of the brick when held flush with the surface of the litter and again after allowing it to exert its full weight. Similar measurements of the F and H layers revealed that compression of these two strata was negligible. In temperate forests, however, this possible source of error was avoided by inserting a plastic ruler into the L layer with the lower end resting against the surface of the F layer. Hence any compression of the F or H layer resulted in a lowering of the bottom of the ruler and the effect was cancelled out. The weight per unit area applied was the same as in Montane Rain Forest but instead of a brick, a spring scales inverted so that the flat platform was the force-exerting surface, was used. The scales were pushed down until the needle pointed to the value on the dial previously calculated to represent 0.025 lbs per cm^2 . Location of sites for measurements were determined in the same fashion as those for measurements of depth.

Mean compressions of class I litters were significantly different from those of class II with the exception of types I Complex and I Curled from Montane Rain Forest which were represented by too few samples for interpretations to be made (Fig. 13). In general, class I had compression values about one-third higher than class II.

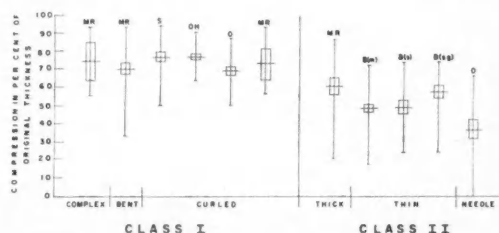


FIG. 13. Compression of litter types in per cent of original thickness. Vertical line represents range, horizontal line the mean, and the rectangle twice the standard error on each side of the mean.

B (m)—Beech-maple forest, mature section
B (s)—Beech-maple forest, sapling section
B (sg)—Beech-maple forest, second-growth section
MR—Montane Rain Forest
O—Oak-pine-aspens forest
OH—Oak-hickory forest
S—Swamp hardwoods

$N = 35$ for Class II except in Montane Rain Forest where $N = 34$. For class I Curled litter, $N = 65$ in Montane Rain Forest, 35 in oak-hickory and oak-pine-aspens, and 40 in the swamp hardwoods. $N = 13$ in I Complex litter, and 8 in I Bent.

With one exception, type II Thick had mean compression values significantly higher than II Thin which in turn had mean values significantly higher than II Needle. The compression values of II Needle litter were surprisingly high (37%). The interstices are small in this type but because of the shape of the needles there are many of them, which probably accounts for the compression values obtained.

The exception noted above was II Thin from the second-growth section of beech-maple forest. It had a mean compression (59%) which was not significantly different from that of I Thick (61%) from Montane Rain Forest. The reason for this relatively high compressibility in the second-growth section of beech-maple may have resulted from the presence of some oak and aspen leaves which have a tendency to curl.

All of the types in class I had mean compression values between 69 and 77%. The mean compression of litter was significantly higher in the oak-hickory area (77%) than in the oak-pine-aspen (69%) although the same type (I Curled) occurred in both. In the former place most of the leaves were oak, whereas in the latter there were many aspen leaves. Aspen leaves usually curled only on the edges whereas the oak leaves commonly rolled up. The difference in relative proportion of oak leaves in these two areas was probably responsible for the differences in compressibility.

An analysis was made of forest floor litter type I Bent and II Thick in which the percentage of dominant leaf forms (flat-leathery and bent-rigid) at a series of sites varied over a wide range. The plots chosen were those along the transect previously mentioned. After estimation of percentage of the two leaf forms present, compression data were taken. The results (Fig. 14) indicated there was a gradual change in compression characteristics depending on the percentage of bent leaves. By the criteria used here for

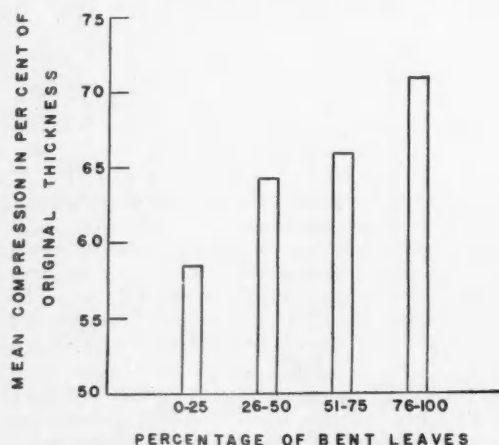


FIG. 14. Compression in per cent of original thickness of various natural mixtures of bent and flat leaves from the floor of Montane Rain Forest. Number of measurements per category ranged from 6 to 37.

distinguishing classes and types (habit of majority of component leaves) the mixtures with less than 65% compression fell in class II (type II Thick), those with compression values greater than 65% in class I (type I Bent). This demonstrates a gradual change in habitat characteristics between different types and classes.

As the mean difference between thickness of the L layer before and after compression is directly proportional to the amount of space in the litter, the former can be used as a measure of the latter. The types of class I tend to have a greater amount of space than those of class II (Table 6). All of the types of class II had a mean difference between compressed and uncompressed thicknesses of 2.5 cm or

TABLE 6. Mean difference between thickness of the L layer before and after compression.

Class	Type	Forest type	Mean difference in thickness of compressed and uncompressed litter (cm)	Range (cm)	N
I	Bent	Montane Rain Forest	3.51±0.52	0.5- 8.0	51
	Curled	Oak-pine-aspen level ground	3.23±0.28	1.5- 5.0	35
		Oak-pine-aspen depressions	5.16±0.48	3.0- 8.5	35
		Montane Rain Forest	4.38±1.99	1.0- 7.5	8
		Swamp hardwoods	2.42±0.16	0.9- 4.3	70
		Oak hickory	3.93±0.35	1.8- 6.0	35
	Complex	Montane Rain Forest	8.50±4.29	3.5-14.0	7
II	Thick	Montane Rain Forest	2.50±0.53	0.5- 7.0	30
	Thin	Beech-maple mature section level ground	1.83±0.14	1.0- 3.5	35
		Beech-maple mature section mounds	1.03±0.14	0.5- 2.0	35
		Beech-maple mature section depressions	3.36±0.40	2.0- 7.5	35
		Beech-maple sapling section	1.56±0.20	0.5- 3.0	35
		Beech-maple second-growth	1.46±0.18	0.5- 2.5	35
	Needle	Oak-pine-aspen	0.80±0.14	0 - 2.0	35

less on level microtopography. The lowest mean value (0.8 cm) occurred in type II Needle which therefore had the least amount of space. Class I had mean values ranging from 2.42 cm (type I Curled in swamp hardwoods) to 8.5 cm (type I Complex in Montane Rain Forest). The size of the interstitial spaces in a litter containing curled, rolled, or bent leaves was much larger than if the leaves were flat. Thus the tendency of leaves to curl or bend in class I litter was undoubtedly responsible for the greater amount of space in this group than in class II.

In mature beech-maple forest, litter on mounds had less space than on level microtopography, whereas litter in depressions had more. The litter type was

the same in all three situations (Table 6). It was previously shown that depressions also had litter which was deeper, and mounds had litter which was shallower, than that on level microtopography. This was probably responsible for the difference noted in the amount of space, as deep accumulations of a given litter type would be expected to have more space than a shallower one.

RELATION BETWEEN DEPTH AND COMPRESSION

During field work it was noticed that except in the dry part of the summer, the bottom of the L layer in the deeper depressions of the oak-pine-aspen area consisted of leaves which had become uncurled and were either flat or slightly concave. They were not fragmented as were the partly decayed leaves of the F layer. Usually the boundary between the curled and the flat leaves was sharp and appeared to coincide with the upper limit at which free water existed in droplets or small pools between the leaves. This condition posed the question whether compression characteristics of a given litter are dependent on depth. It is conceivable that the bottom leaves are flattened out by the weight of those above and hence deep accumulations might have proportionately lower compression values than shallow ones. However, when the compression values used in the above analysis were plotted against their corresponding initial depths, a general scattering of points occurred and no trend was evident. The communities from which litter was tested in this manner were oak-hickory, beech-maple (mature, sapling, and second-growth sections), swamp hardwoods, oak-pine-aspen (types I Curled and II Needle), and Montane Rain Forest (types I Bent and II Thick). Thus the flattening effect is not a general characteristic and is probably confined to deep depressions where water drains in and accumulates between the leaves, causing them to uncurl.

SEASONAL CHANGE IN LITTER DEPTH

Any comparison of the L layer in deciduous and evergreen forests must take into account the rapid change in litter depth caused by seasonal shedding of leaves in the former. Of the temperate forests in which studies were carried out, only the oak-pine-aspen community contained a large percentage of evergreen species. Most of the tree species in Montane Rain Forest were evergreen although there were a few seasonally deciduous ones. In the swamp hardwoods and beech-maple forest, an increase in litter depth of more than 100% of the original value occurred during the period of leaf fall in 1957 but decreased again by about half within 1 year. There were two processes probably involved in this reduction of litter depth: fragmentation of the bottom leaves to form the F layer, and compaction of the loose layer of newly fallen leaves by snow during the winter. However, separating the effects of these two factors is beyond the scope of the present study and

the important point to be emphasized for these two forests is the rapid increase in litter depth in the autumn and its subsequent decrease throughout the rest of the year.

There was a net increase in litter depth in both forests between late summer, 1957, and the same season of 1958. Average depth in mature beech-maple was 2.3 cm in 1957 and 3.1 cm in 1958. Corresponding values for the swamp hardwoods were 1.5 cm and 3.0 cm respectively. The differences between the two years were significant. This increase indicates that more litter accumulated during the autumn of 1957 than was reduced by humification through the subsequent year.

In 1957 and 1958 depth of the leaf litter was measured in the beech-maple forest and elevated areas in the swamp hardwoods during the late summer before leaf-fall had occurred. Also, the depth of the layer of newly fallen leaves was measured in both areas just after abscission in 1957. All measurements were taken when the litter was dry and hence differences in depth did not result from differences in moisture conditions.

Data on seasonal or yearly differences in litter depth are not on hand for the Montane Rain Forest. However, although certain species of trees shed their leaves seasonally, the forest as a whole is evergreen and leaf fall is more of a continual process resulting in a gradual, if any, change in litter depth over a long period of time.

DISCUSSION

The amount and form of organic material present determines the suitability of the forest floor as a habitat for various types of organisms and results from a number of processes, including accumulation, transport, humification, and mineralization. The rates at which these occur are influenced by temperature, moisture, and activity of microorganisms. In many tropical forests, leaf fall is constantly in progress but decay is rapid. Humification and mineralization proceed at high rates, the latter often occurring as rapidly as the former, resulting in the destruction of humus as fast as it forms (Richards 1952).

In Montane Rain Forest, evidences of this are seen in the many bare patches which are present, although temperatures there are relatively low in comparison with most lowland tropical areas. Another factor, transport, probably is also involved. Shortly after rains the small mountain streams become greatly swollen as a result of the rapid runoff from the steep slopes covered with saturated soil. The fine organic particles are probably carried along and perhaps also the larger objects like sticks and leaves, although this aspect has been virtually unstudied. Transport by wind is probably not important in the Montane Rain Forest under consideration.

In temperate regions the same factors are at work, although accumulation is seasonal except in conifer-

ous forests. The rate of humification and mineralization is slower because of the cold winter period and hence organic material tends to accumulate, in some forests as distinct layers, in others mixed into the mineral soil by animals. The process of decay is also different, being carried out in the tropics chiefly by bacteria but in temperate areas mostly by fungi (Richards 1952, Lutz & Chandler 1955). Moisture and temperature profoundly affect the process of decay and mineralization and consequently the end product in the tropics differs from those in temperate regions (Senstius 1958). Transport by water in the temperate areas studied in the present investigation is probably relatively slight although wind may be an important factor in oak-pine-aspen forest.

The various structural features of the litter are modified by many factors and the resulting spatial configuration is biologically important. Litters with bent or curled leaves have a greater amount of space available to organisms than those in which the leaves lie flat. The latter type of litter imposes the restriction that its resident organisms be small or else strong enough to rearrange the litter structure in accordance with their demands. On the other hand, large interstitial spaces permit more rapid evaporation than smaller ones, if other factors remain the same, and favor greater penetration of water during rains.

A given amount of interstitial space may mean various things in different kinds of litter. It may either indicate many small spaces or a few large ones in the litter layer in question. For this reason compression characteristics are presented as well as measures of litter depth and actual amount of space. The compression values are characteristic for a given litter type and are dependent on the structure, whereas amount of space in the L layer depends partly on structure and partly on depth of litter. Depth is also an expression of the structure of the litter in that the loose types tend to be deeper than more compact ones. Depth also depends on local conditions of accumulation and decay. In litters of comparable structure, the deeper ones provide more space available to organisms.

The effect of form, texture, and degree of cutinization of component leaves on litter structure was discussed. It suffices here to point out that the sclerophyllous condition of many tropical leaves influences humus texture in that, although humification is generally rapid, certain parts of such leaves are only slowly destructible and pass into the humus layers as coarse particles. These persist, being less subject to transport by water than finer particles and are probably responsible for the coarse appearance of humus in the Montane Rain Forest. Humus in the temperate forests studied is finely divided and much more uniform.

All the leaves which were studied pass through similar stages of decay in that they first fragment into smaller pieces which are still recognizable as to origin, and finally break down into particulate matter.

The thin leaves probably decay faster than those which are thicker and more heavily cutinized. However, no quantitative data were gathered on comparative rates of decay of different kinds of leaves. The wetter forests probably allow more rapid decay than the drier oak-hickory or oak-pine-aspen. In the inundated depressions of the swamp hardwoods, almost complete decay of the litter accumulating in the autumn occurs within one year.

In this paper mechanical and structural factors have been emphasized. This is not an attempt to minimize the importance of chemical, biotic, or moisture conditions to the forest floor fauna. These factors are often critical and have received much attention in the literature, perhaps to the neglect of structural ones. However, a habitat is most easily recognized and described by its physical features and unless other characteristics are obvious from casual inspection, they are of doubtful use in a classification such as the one presented here.

SUMMARY

A classification of the L layer of the forest floor based on physical characteristics important to animal inhabitants was developed. Class I was composed of leaves which were rolled, curled, or bent into a V in cross section. It had large, round or angular interstices. Class II was composed of leaves lying flat upon each other. It had small, flat interstices. In general, Class I litter tended to occur in deeper accumulations than Class II and had a greater compressibility and a larger volume of interstitial space. Class III was made up of solid objects such as logs. Each class contained several types, recognized by the habit of the majority of component leaves.

The floor of the Montane Rain Forest had a much greater percentage of the area occupied by bare soil and exposed F and H layers than the temperate forests studied. It also had a larger number of litter types. In Montane Rain Forest and oak-pine-aspen forest, the litter was distributed in a mosaic pattern but was rather uniform in the beech-maple and swamp hardwoods. Montane Rain Forest had a thinner F layer than the temperate forests studied, but where an H layer occurred it was as thick on the average as those in the temperate ones.

Microtopographical differences and differences in herb cover affected the litter structure. Herbaceous vegetation tended to prevent leaves from settling, and caused a loosely structured litter. Depressions had thicker L, F, and H layers and root mats than level ground, whereas mounds had thinner ones.

The deciduous and oak-pine-aspen forests displayed great seasonal fluctuation in volume of litter. In the beech-maple forest and hardwood swamp there was a net increase from 1957 to 1958. If the forests studied are arranged in descending order of total volume of forest floor habitat, they are oak-hickory, Montane Rain Forest, beech-maple, and oak-pine-aspen. Calculations were not made for the swamp hardwoods.

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THE ECOLOGY OF BLACKBIRD (*AGELAIUS*) SOCIAL SYSTEMS

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TABLE OF CONTENTS

	PAGE		PAGE
INTRODUCTION	285	Initiation of Breeding	295
STUDY AREAS	286	Nesting Habitat	297
METHODS	287	Time of Breeding	297
GENERAL BIOLOGY OF THE SPECIES	287	Territory	298
THE SOCIAL SYSTEMS	289	Mating System	299
1. The Red-winged Blackbird		Clutch Size	300
Non-breeding Period	289	Nesting Success	300
Initiation of Breeding	290	Feeding Behavior of Adults	301
Nesting Habitat	290	Colony-size Limitation	301
Time of Breeding	290		
Territory	292	TIME AND ENERGY BUDGETS	302
Mating System	294	THE EVOLUTION OF MATING SYSTEMS	306
Clutch Size and Nesting Success	294	THE EVOLUTION OF BLACKBIRD SOCIAL SYSTEMS	308
Feeding Behavior of Adults	294	SUMMARY	310
2. The Tricolored Blackbird		LITERATURE CITED	311
Non-breeding Period	295		

INTRODUCTION

The conspicuousness of adaptive radiation in morphology tends to conceal the fact that often the slight differences between closely related species give no clues to their widely differing ecologies, because many of the important differences between species are the result of behavioral and not morphological adaptations. This study analyses the role of social organization of the Red-winged Blackbird (*Agelaius phoeniceus*) and the Tricolored Blackbird (*A. tricolor*) in the different ways in which these two species exploit their environment.

Knowledge of avian social systems began with natural history studies, but certain phases, such as territoriality, early attracted special consideration. In the 1930s, social systems began to be studied from the viewpoint of the comparative ethologist, who is primarily interested in the motivational and evolutionary aspects of behavior patterns, but whose publications contain a wealth of information about many ecological features of avian social systems. The mathematical approach to population parameters has provided a basis for considering the consequences of changes in social system characteristics upon basic population parameters, but biologists have in general been suspicious of this approach, which seemed to rest upon assumptions of doubtful biological validity. The result is rather widespread failure to realize the significance of certain features of social systems in quantitative terms, and failure to record and publish relevant information. Finally, the study of social

systems from the modern ecological viewpoint has lagged behind other approaches because few observers have made use of the background of a century of Darwinian thinking in evaluating their observations.

In this study I have considered all features of social systems to be the products of natural selection just as are any physiological or morphological adaptations. To the question whether or not differences between social systems are adaptive, three types of answers are possible. Firstly, it may be assumed that the particular features of a social system are surely adaptive. Secondly, it may be assumed that the traits are purely fortuitous, without selective significance. Thirdly, it may be assumed that the particular traits are not adaptive but that they are associated with other, as yet unrecognized, differences which are adaptive (Maynard Smith 1958). In this paper I shall attempt to interpret as far as possible the characteristics of social systems in the light of the first of these three assumptions. The second is rejected because it is sterile as a basis for research and because the widespread and consistent differences to be discussed cannot be without selective significance. The third can never be easily accepted, for unless this statement of faith is followed by attempts to discover the traits of adaptive significance and their connection with the supposedly unadaptive trait, nothing is really explained. Furthermore, no such case involving polygenic traits has been shown to be true, and separation of desirable from undesirable traits will almost certainly occur with time.

Because the closely related and morphologically similar Red-winged and Tricolored blackbirds differ

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strikingly in their social organization, they are excellently suited to studies developed from the premises just given. Furthermore, these and other species of the family Icteridae are common, easily observed, and well-known. Moreover, their social systems range from routine territoriality to extreme coloniality and from monogamy to promiscuity and parasitism. My studies of these two blackbird species were carried out in north-central California from 1957 through the spring of 1960. The behavioral aspects of this investigation are being treated separately, and a report on autumnal breeding in the Tricolored Blackbird has already been published (Orians 1960).

This entire study was conducted under the supervision and guidance of F. A. Pitelka. The manuscript has also been read by P. Marler and G. L. Stebbins, both of whom have made valuable suggestions. Field work was made possible through the cooperation of F. Barnett of Lodoga, California, and C. Haskell of Marysville, who permitted access to their excellent marshes and also kindly provided lodging. A. S. Leopold generously made available his notes on blackbird activity at the Haskell Ranch since 1954. J. Parker of the East Bay Regional Park District permitted me to erect an observation tower on the small marsh at Jewel Lake during the spring of 1958. G. M. Christman aided in the preparation of the illustrations and provided data on Californian Indians. At many times during the course of this study I was aided in the field by fellow graduate students, including J. L. Brown, R. B. Root, E. O. Willis, M. Konishi, N. K. Johnson, D. R. Medina and J. Frost. Exchange of ideas with G. Collier, who is studying different aspects of the same species at Los Angeles, has been a helpful stimulus. For the two academic years 1958-1960 I was supported by a National Science Foundation Graduate Fellowship which permitted me to spend extensive periods in the field during the blackbird breeding season. Travel expenses were in part defrayed by a grant from the Museum of Vertebrate Zoology. Finally, my wife helped type the manuscript. To all I express my sincere appreciation.

STUDY AREAS

Field work was concentrated at four main areas, with supplementary observations at other localities (Fig. 1). Studies were first begun at Jewel Lake, Tilden Regional Park, Contra Costa County, in 1957. The lake, formed by a dam constructed across Wildcat Creek in the Berkeley Hills about 1900, has a maximum depth of 10 ft and is about 510 ft above sea level (Gullion 1953). About one-third of its 2.7 acres is filled with emergent vegetation, chiefly cattails (*Typha angustifolia* and *T. latifolia*), in which Redwings nest. No Tricolored Blackbirds breed there though occasional individuals roost in the autumn and winter. During the non-breeding season the marsh harbors a large roost of male Redwings, but females are normally present only during the nesting season. This marsh was studied intensively during 1958 and less frequently in 1959 and 1960.



Fig. 1. Study areas in central coastal California. Jewel Lake is marked by the large "X," the East Park Reservoir by the large circle, and the Haskell Ranch by the large square. Other study areas are indicated by small dots. Areas of large breeding concentrations of Tricolored Blackbirds are shown by diagonal lines.

Both species of blackbirds breed commonly at the East Park Reservoir in the Coast Ranges of Colusa County, a body of water formed in 1910 by a dam across Stony Creek. Because its waters are used to irrigate orchards in the Sacramento Valley near Orland, in the summer it may be reduced to a mere remnant of its winter size and, as happened in 1959, may completely dry up. Most of the shoreline of this large reservoir is devoid of emergent vegetation but there are two large marshes where two major streams enter it. In addition, there are small patches of cattails in some of the indentations along the shores (Fig. 2). The reservoir is surrounded chiefly by heavily grazed blue oak (*Quercus douglasii*) parkland, chaparral (chiefly chamise, *Adenostema fasciculatum*), and, at the south end, by cultivated fields. I first visited the area briefly in 1957 and 1958, but at the end of March, 1959, I established a camp on the shores of the reservoir which served as a base for field work through the breeding season. By early June the water had already dropped to such a low level that no blackbirds remained there. Before the reservoir completely refilled in March of 1960, the cattails in the marsh at the southeast end were completely burned. Blackbirds began to breed as soon as new growth permitted and regular observations were also made throughout the second spring.

The Haskell Ranch, eight miles southeast of Marysville, Yuba County, is located in the heart of a ranching district. The marsh is surrounded by irrigated pastures and owes its existence to the run-off



FIG. 2. Two of the isolated patches of cattails at the East Park Reservoir, Colusa County, California, April, 1959.

of excess water from them. It is burned every winter or early spring and cattails are cut to keep certain water areas open for duck hunting. None of these activities greatly influences the blackbirds, however, as the cattails sprout immediately following burning and there are always large areas which are not cut. Both Redwings and Tricoloreds breed there, and sometimes Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) as well, though they were absent in 1959 and 1960. My studies were limited to these two years, though Dr. Leopold's notes were available for earlier years.

Observations were made during May and June, 1959, and throughout the fall, winter, and spring of 1959-1960 in the rice-growing and duck-hunting areas of Colusa and Glenn counties where extensive areas of cattails are maintained as duck habitat. Also, the rice fields are favorite feeding grounds for Tricolored Blackbirds, so that this region supports large populations of this species, Redwings and smaller numbers of Yellow-heads.

In addition to these four major study areas, observations were made in the rice-fields in Sacramento County and in the course of road travel between the study areas. Prospecting trips were made to other areas in the valley and foothills during each spring, and in 1958, an exploratory visit was made to areas in the San Joaquin Valley and foothills of the Sierra Nevada. Upland breeding Redwings were also briefly observed on Brooks Island in San Francisco Bay.

METHODS

The basic method in this study was simply to record in detail all features of social organization seen in the field, though advantage was taken of natural experiments offered by habitat differences, variations in weather, and human interference. In addition, I conducted elimination experiments in 1959 and 1960 to study repopulation. Each of the major displays and vocalizations of both species was assigned a symbol which enabled me to record more fully the activities of an individual bird as long as it remained in view. At Jewel Lake in 1958, I watched male Redwings several mornings each week throughout the breeding season. Less extensive observations were made in the afternoons. Extensive use has been made of these observations and the samples of activity sequences they include in the development of time and energy budgets. Particular attention was paid to the temporal and spatial aspects of social organization, as these are two features in which the two species differ most strikingly.

GENERAL BIOLOGY OF THE SPECIES

The widespread Redwing breeds from the Atlantic to the Pacific and from Central America almost to the Arctic Circle in west-central Canada (Bent 1958). Most individuals migrate from the colder portions of the range in the winter but some of the southern races, including the Californian ones, are resident. The Tricolored Blackbird has a much more restricted distribution, breeding from southern Oregon and the Modoc Plateau of northeastern California, south through the lowlands of California west of the Sierra Nevada to northwestern Baja California (Grinnell & Miller 1944). The species is not migratory but is nomadic and highly colonial (Fig. 3), though the pattern of nomadism is poorly known. Large flocks appear suddenly in areas from which they have been absent for months, they breed, and then quickly withdraw. Size and location of colonies vary from year to year, though certain sites, such as the East Park Reservoir and the Haskell Ranch, are regularly used. In his extensive studies of Tricolor distribu-



FIG. 3. The Marysville Tricolor colony during the nest building period, Yuba County, California, May, 1959.

tion, Neff (1937) observed striking shifts in the location of colonies in the Sacramento Valley (Table 1), and to show that the variation is not simply due to variability in searching time, I have recalculated his data to express it as thousands of nests discovered per man-day spent searching (Table 2).

TABLE 1. Estimated nesting populations of *Agelaius tricolor* (figures represent thousands of nests; data from Neff 1937).

County	1931	1932	1933	1934	1935	1936
Butte.....	—	28	106	32	3	4
Colusa.....	—	32	16	37	3	5
Glenn.....	—	68	61	282	4	4.5
Merced.....	—	50	58	2	37	10
Sacramento.....	—	121	101	80	1	15
Sutter.....	—	10	13	6	1	3
Yolo.....	10	38	3	2	10	2
Yuba.....	113	2	7	50	5	5

TABLE 2. Thousands of nests discovered per man-day expended (calculated from data given in Neff 1937).

County	1931	1932	1933	1934	1935	1936
Butte.....	0	9.3	26.5	16.0	1.5	4.0
Colusa.....	0	10.7	5.3	18.5	1.5	5.0
Glenn.....	0	11.3	6.1	6.3	2.0	2.3
Merced.....	—	50.0	1.9	0.7	7.4	2.5
Sacramento.....	0	24.2	33.7	26.7	0.5	3.0
Sutter.....	0	5.2	6.5	6.0	1.0	3.0
Yolo.....	0.2	12.7	1.0	1.0	5.0	1.0
Yuba.....	1.9	0.03	0.1	0.8	0.1	2.5

The plumage of these two species is so similar that museum specimens are sometimes misidentified. The adult male Tricolor has a bluish luster to its black plumage, and the red of the epaulets is a dull crimson in contrast to the bright scarlet of the male Redwing. The most conspicuous feature of the male plumage, and the one which gives the species its common and scientific names, is the broad white border to the middle wing coverts. In most races of the Redwing these feathers are tipped with buffy, but in those races occupying the central Coast Ranges and Great Valley of California, the metropolis of the Tricolor, they are black so that the wing lacks the light stripe. This plumage difference between males is not only conspicuous to the human observer, it is the most important means of species identification used by the birds themselves. Occasional Redwings in a flock of Tricolors are singled out for special attack by a resident male Redwing in whose territory the flock lands.

Females are less easily distinguished because, although female Tricolors are darker than most races of the Redwing, in the area of distributional overlap female Redwings are the darkest of that species. Thus, the need of making accurate specific identification notwithstanding, there is a convergence of female plumage in the area of sympatry in contrast to the

TABLE 3. Comparative measurements of blackbirds.

Measurement	Species	Sex	Mean (mm)	Standard deviation (mm)	Range (mm)
Wing.....	Redwing	♂♂	124.5	2.4	118.8-131.6
		♀♀	102.9	2.6	97.5-108.5
	Tricolor	♂♂	120.8	2.1	115.5-125.2
Tail.....	Redwing	♀♀	105.2	2.1	102.2-111.2
		♂♂	84.7	3.6	75.9-93.8
	Tricolor	♂♂	81.1	3.1	75.4-89.7
Tarsus.....	Redwing	♀♀	68.9	2.3	64.0-78.6
		♂♂	28.2	1.1	25.0-32.8
	Tricolor	♀♀	24.9	0.9	22.5-26.6
Culmen.....	Redwing	♂♂	28.1	1.0	26.6-30.4
		♀♀	25.2	0.8	23.1-26.8
	Tricolor	♂♂	22.6	1.1	19.8-24.9
Bill depth.....	Redwing	♀♀	19.4	0.9	17.5-22.2
		♂♂	24.5	1.0	22.4-27.3
	Tricolor	♀♀	21.8	1.0	19.8-24.5
	Redwing	♂♂	8.7	0.5	7.6-10.1
		♀♀	7.5	0.5	6.1-8.3
	Tricolor	♂♂	8.0	0.3	7.5-8.5
		♀♀	6.9	0.8	6.3-8.0

divergence in the males. In general, female Tricolors are more uniformly sooty than female Redwings, there being less contrast between throat and breast. In the autumn, female Redwings are strongly tinged with rusty on the back, a feature never shown by the female Tricolor.

Sexual dimorphism in size, though great in both species, is less in the Tricolored Blackbird. Measurements of winter and spring specimens of both species are given in Table 3. In these specimens the male Tricolors are smaller than male Redwings in wing, tail, tarsus, and bill depth, but are larger in culmen. On the other hand, female Tricolors are larger than female Redwings in wing, tail, tarsus, and culmen, but are smaller in bill depth. This longer, narrower bill of the Tricolor is one of the most reliable morphological differences between the species.

The comparative weights of the two species are less certain. Among the MVZ specimens the male Tricolors average heavier than male Redwings and females heavier than female Redwings. However, in a sample of 47 male Tricolors and 31 male Redwings collected in the Sacramento Valley in October and November, 1959, the male Tricolors averaged lighter than the male Redwings, the difference being due to a decrease in the mean weight of male Tricolors.

Specimens collected in the autumn of 1959 were also measured for wing spread, maximum wing width, and total wing area. Wing spread and wing width are the same in females but the male Redwing has a greater wing spread and broader wings than the male Tricolor (Table 4). As a result, the Tricolor carries more weight per unit of wing surface than the Redwing (Table 5). The slender, more pointed wing of the Tricolor is conspicuous enough in the field to enable an experienced observer to identify the species at great distances.

As will be discussed later, the roles of the sexes are more similar in the Tricolor than in the Redwing and the species is less polygamous. The lesser degree

TABLE 4. Wing measurement of blackbirds.

Measurement	Species	Sex	Mean (mm)	Standard deviation (mm)	Range (mm)
Wing spread....	Redwing	♂♂	15.4 in.	.30	15.0-16.1
		♀♀	13.2	.23	12.7-13.3
	Tricolor	♂♂	15.1	.19	14.8-15.6
		♀♀	13.2	.27	12.7-13.7
Wing width.....	Redwing	♂♂	3.9 in.	.11	3.7- 4.1
		♀♀	3.2	.10	3.0- 3.3
	Tricolor	♂♂	3.5	.10	3.4- 3.7
		♀♀	3.1	.12	2.9- 3.5
Wing area.....	Redwing	♂♂	45.5 sq. in.	2.05	42.4-50.4
		♀♀	31.4	1.12	28.6-33.0
	Tricolor	♂♂	39.4	2.17	36.2-42.6
		♀♀	29.6	1.31	27.2-32.4

TABLE 5. Wing loading.

Species	Sex	Mean wing (sq. in.)	Mean weight (g)	Weight per square inch of wing surface (g)
Redwing....	Male	45.5	66.1	1.45
	Female	31.4	42.4	1.35
Tricolor.....	Male	39.4	63.3	1.60
	Female	29.6	46.5	1.57

of sexual dimorphism in size thus fits in with the general picture in the Icteridae, where there is a correlation between the degree of size dimorphism and the extent of promiscuity (Selander 1958). The Tricolored Blackbird not only travels extensively during its nomadic wanderings, but both sexes fly great distances when gathering food for the young, a time when speed is of great importance. The narrow, more pointed wing has probably evolved in response to this need as it has in other avian groups. The Redwing male does not feed the nestlings, but engages in frequent conspicuous display flights over the territory. The broad wing is therefore useful as a display organ. The Tricolor has no such aerial displays.

THE SOCIAL SYSTEMS

1. THE RED-WINGED BLACKBIRD

Non-breeding Period. Outside the breeding season Redwings are highly gregarious, travelling and feeding in flocks of varying size, and roosting together in favored sites, usually over water, which attract birds from distances up to twenty miles or more. On evenings for which counts of roosting birds, mostly males, were made at Jewel Lake, the total number varied between 1,544 and 2,596; the number of flocks between 159 and 205; and the average flock size from 8.6 to 14.1 (Table 6). Flocks were smaller at the beginning and end of the roosting time, and the rate of flock arrival was greatest in the middle, so that the bulk of the birds arrived in a short period of time (Fig. 4). Arrival time, which closely fol-

TABLE 6. Evening roosting of Redwings, Jewel Lake, fall, 1958.

Date	10/16	10/23	11/6	11/13	11/20	11/27	12/4
Number of birds....	1,544	1,368	2,134	2,296	1,701	1,686	2,596
Number of flocks....	173	159	205	191	152	173	184
Average flock size....	8.9	8.6	10.4	12.0	11.2	9.7	14.1

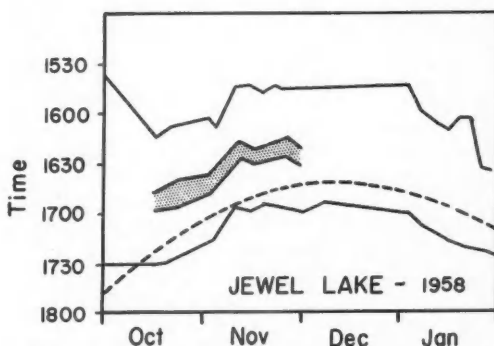


FIG. 4. Roosting of male Redwings at Jewel Lake. Solid lines indicate the arrival of the first and last roosting birds. The time of local sunset is shown by the dashed line. The period during which at least one-half of the birds arrived is indicated by the dotted area.

lowed the time of local sunset, was usually spread out over about one and one-half hours.

Enormous numbers of blackbirds roosted at the Colusa marsh in the autumn of 1959. Redwings and Tricolors were by far the most numerous but there were also many Brewer Blackbirds (*Euphagus cyanocephalus*), Cowbirds (*Molothrus ater*), Yellowheads and Starlings (*Sturnus vulgaris*). This roost attracted birds from an enormous area from the Sacramento River west to the foothills of the Coast Ranges and for at least ten miles north and south of the marsh. During the major part of the roosting flight on the evening of October 15, I estimated that 500-1000 birds per second were crossing a road south of the marsh, so that perhaps 750,000-1,500,000 birds entered the roost from that direction during the 25-minute period of maximum arrival. Since large flocks were also approaching the marsh from other directions as well, at least several million birds were roosting there at this time.

Whereas birds straggled in for over an hour in the evening, the morning exodus lasted only about 30 minutes. After the main morning feeding, the birds returned to the cattails where they rested, preened, sang, and bathed for much of the remainder of the day. Another major feeding flight in mid-afternoon preceded roosting for the night. Though the marsh was always full of birds at mid-day, there was a steady movement in and out and individual birds probably fed at least once each day in addition to the two main feeding periods.

A striking feature of Redwing social organization during the fall and winter is the segregation of

the sexes which, though by no means complete, is very pronounced. As already mentioned very few females roosted at Jewel Lake, and though both sexes roosted abundantly at Colusa, most flocks seen feeding during the day were wholly or largely composed of one sex.

The enormous numbers of Redwings in the Sacramento Valley in the autumn obtain most of their food from agricultural land. I did not examine any stomachs, but by observing feeding birds it is easy to determine what they are taking. In late summer the birds concentrate upon seeds of the water grass (*Echinochloa crusgalli*), which is abundant around the edges of all rice fields and ditches in irrigated country, and rice, which is then coming into the milk stage. The greatest damage to the rice occurs at this time though the birds continue to utilize it heavily until it is harvested. Mechanical methods of harvesting rice leave large amounts of grain scattered on the ground among the stubble which the blackbirds continue to use until the fields are plowed. At this time of year, newly sprouting alfalfa fields are also used as sources of insects. As the autumn progresses, more and more fields are harvested and plowed, and feeding conditions become progressively worse. This is partly offset by the flooding of many fields to attract ducks for hunting, because these fields are not plowed and also produce many insects. Nonetheless, by early January the populations of Redwings and Tricolors in the Sacramento Valley are greatly reduced from their mid-autumn level. One can drive great distances in late winter and see few blackbirds where earlier there had been millions. It is not certain where they go at this time, but they probably move to the San Joaquin Valley and other areas to the south where agricultural practices are different.

Initiation of Breeding. The onset of the breeding period in the Redwing is marked by the establishment of territories by the males early in January in north-central California. At first the territories are occupied for only brief periods in the early morning and late afternoon, but gradually the amount of time spent there increases until the birds are present on or near the territories all day. At Jewel Lake in the winter, territorial males roost in the marsh together with a large number of birds which leave to nest elsewhere. The resident males briefly remain on their territories after the roosting birds have left, and then also leave for the rest of the day to feed (Fig. 5). It is not until mid-March that the males begin to feed in the area and not until early April that they remain all day and find the bulk of their food either on the territory or close to it. Females begin to arrive in early March, and by the end of the month most of them roost in the marsh with the males.

At the East Park Reservoir the initiation of the breeding season follows the same general pattern as at Jewel Lake except that events occur about two weeks later. Nights are much colder and vegetational development slower in the foothills than in Berkeley, where the influence of the Pacific Ocean moderates

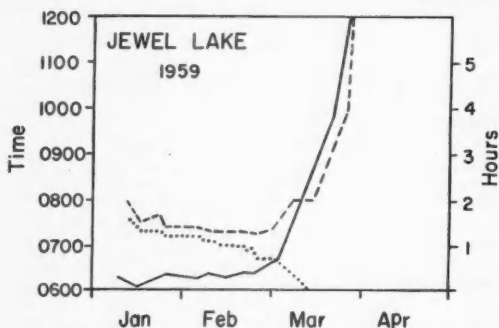


FIG. 5. Occupation of territories by male Redwings. The departure of the main roosting flock is shown by the dotted line; the departure of the territorial males by the dashed line; and the difference in departure time by the solid line.

late winter and early spring temperatures. However, the pattern at East Park Reservoir is also modified by other factors such as the rate at which the reservoir refills and the incidence of burning. In 1960 it was not until mid-March that the cattail marshes were completely reflooded, and no birds roosted there prior to that time. Burning results in the destruction of roosting and nesting cover, which delays the onset of breeding as the birds must wait until the new growth of cattails is high enough to support their nests. In normal years the first nests are constructed in dead cattails.

Nesting Habitat. Redwings nest in a wide variety of habitats (Allen 1914, Sherman 1932, Todd 1940, Nero 1956a), but most nests are located in emergent vegetation, particularly cattails. In California they commonly nest in vegetation bordering irrigation ditches, roadside and fencerow vegetation, riparian situations, weed and brush patches, cropland such as alfalfa and cereal grains, and even upland areas of mixed chaparral and grass. The chief requirement is apparently vegetation strong enough to support the nest surrounded by suitable feeding grounds. Burned cattail areas are used before the new growth sprouts if enough charred stumps remain. In fact, at the East Park Reservoir in 1959, burned areas were chosen instead of dense, unburned patches when both were available on one marsh area. On Brooks Island, the Redwing is a common breeding bird throughout the island, nests being located in bushes of poison oak (*Rhus diversiloba*) and coyote brush (*Baccharis pilularis*) even on the tops of the main ridges. I have not found this situation duplicated elsewhere, but I know of no mainland area with such varied, ungrazed vegetation as is found on the island.

Time of Breeding. The most complete studies of breeding chronologies were made at Jewel Lake in 1958 and East Park Reservoir in 1959. The major features of the breeding season for both areas are summarized in Figs. 6 and 7. Less complete observations at Jewel Lake in 1957 and 1959 show that, with minor modifications, the same pattern held for those

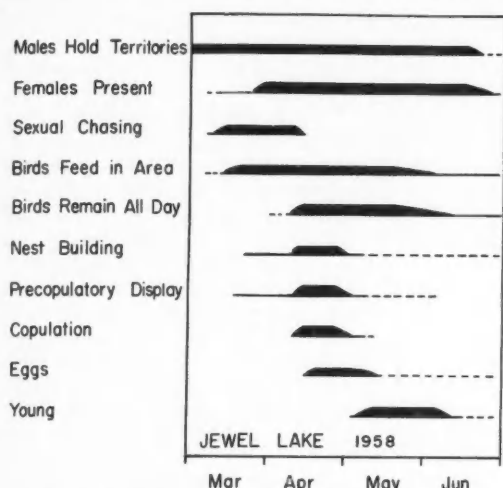


FIG. 6. Breeding chronology of Redwings, Jewel Lake, 1958.

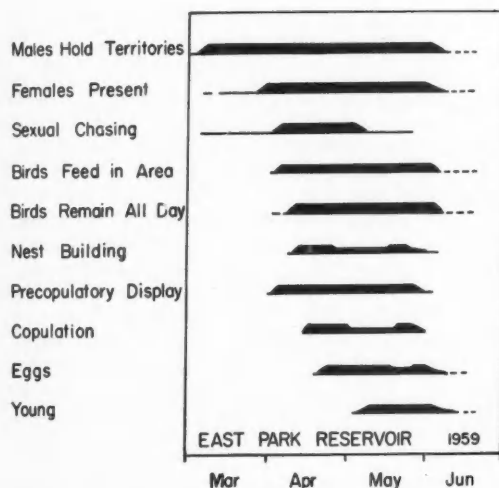


FIG. 7. Breeding chronology of Redwings, East Park Reservoir, 1959.

years as well. For example, the arrival of females, the beginning of chasing of the females by the males and the start of precopulatory displays were within one week of their 1958 time in 1959. Egg-laying in 1957 began two days earlier than in 1958. Because of burning, events were delayed in 1960 at the East Park Reservoir, but in the unburned areas, nesting began four days earlier than in 1959.

A general picture of timing of breeding in the Sacramento Valley was obtained by a census of territorial males along 60 miles of highway between Vacaville and Williams on the west side of the valley. The census area traversed irrigated and non-irrigated cropland and orchards not all of which were suitable blackbird habitat. Territorial males were counted

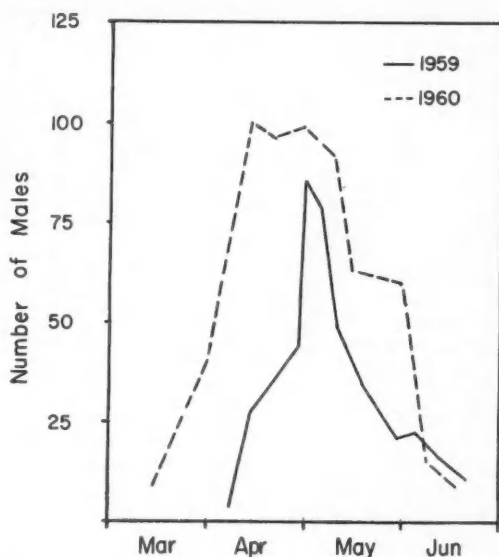


FIG. 8. Territorial male Redwings along 60 miles of highway on the west side of the Sacramento Valley. Birds were counted from an automobile travelling approximately 45 miles per hour.

from an automobile travelling approximately 45 miles per hour. Such a census can give only relative numbers but it does provide a rough picture of time of breeding in the area sampled (Fig. 8). Two points are of interest. Firstly, there is a sharp reduction in the number of birds in mid-May when many of the crops are cut, destroying nesting sites. Secondly, there is only a short period of time during which many birds are present. In 1960, the relatively longer plateau of high numbers was maintained only through continual occupation of new sites throughout the period, since cutting of crops and progressive destruction of nesting areas began in late April. Relatively few sites were suitable for a long enough period to permit the completion of the breeding cycle. Elsewhere in the valley, also, many nests were destroyed before the young had fledged, and though there are no quantitative data, it is quite certain that reproductive success in crop-nesting Redwings is generally poorer than in marsh-nesting birds.

At the East Park Reservoir in 1959, territories on the periphery of the marsh were occupied first and these areas were the most fiercely contested throughout the breeding season. As early as February 19, males displayed in the strip of marsh adjacent to the road for over three hours and more territories were set up than were maintained (Fig. 9). Once six males engaged in vigorous communal displays on the road, walking around each other in full song spread. The time of territory establishment by females and the start of nest building paralleled the pattern of territory establishment by the males.

Normally the females in a given marsh are out of phase with each other (Nero 1956b), but syn-

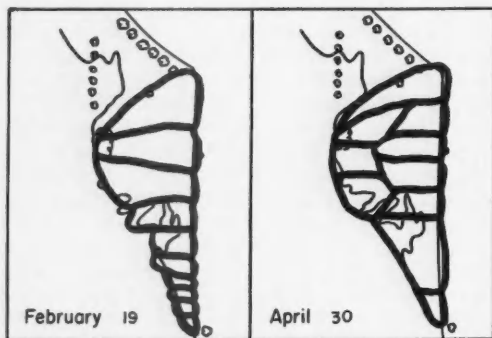


FIG. 9. Size of Redwing territories, East Park Reservoir, 1959.

chrony may be notable at the start of the breeding period. Most females began to nest at about the same time in 1959 in the isolated patches of cattails along the east shore of the East Park Reservoir. Even when all seven patches are lumped together, 51 of 72 nests were started within three days of each other (Fig. 10). It follows that most males in these areas were copulating with more than one female during the same period. Because of nest fail-

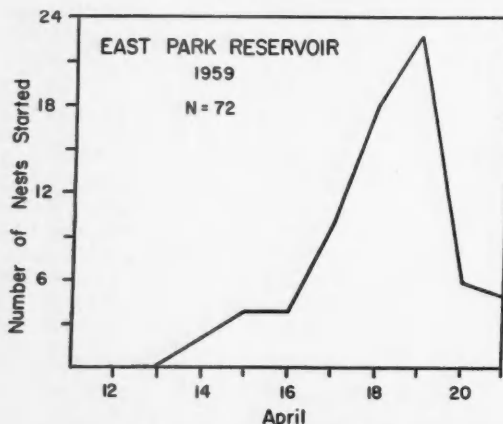


FIG. 10. Breeding synchrony among Redwings in the isolated cattail patches at the East Park Reservoir. The graph is a composite curve representing the pooled data from all seven cattail groups.

ure, second nestings, and the arrival of new females, nestings went out of phase so that by May 15 there were some nests in all stages of construction, others with eggs and young, and free-flying young in the same areas. A check of 30 nests at the Haskell Ranch on May 13 gave a similarly asynchronous picture.

Territory. The territories of the males are defended by means of song, displays and chasing, but little is known about the variations in territory size and the factors influencing them. Linford (1935) found that territories of polygamous males were

twice the size of those of monogamous males, but Nero (1956b) found no such relationship. I also failed to find any correlation between number of females and territory size.

The East Park Reservoir afforded the opportunity to study territory size in marsh areas of contrasting characteristics. Progressively more food is obtained on the territories in the small clumps of isolated cattails, the peripheral strips of cattails along the main marsh, and the main marsh itself, in that order. Territories were substantially the smallest in the isolated cattail clumps, larger in the peripheral strips, and largest in the main marsh (Table 7). Territory size was also determined for a portion of the Haskell Ranch marsh for both 1959 and 1960. In 1959, territories averaged larger than at the East Park Reservoir; but in 1960, they were comparable to territories at the periphery of the main marsh at the reservoir (Table 8). There are no other data from the valley floor with which to compare the results obtained at

TABLE 7. Size of Red-winged Blackbird territories, East Park Reservoir, 1959.

Situation	Number of territories	Average size (sq. ft.)
Isolated cattail clumps surrounded by grassland.....	21	2,512
Strip of marsh at the edge of the reservoir.....	17	8,477
Main marsh area, including both central and peripheral territories.....	22	10,653

TABLE 8. Size of Red-winged Blackbird territories, Haskell Ranch.

Year	Number of territories	Average size (sq. ft.)
1959.....	10	13,720
1960.....	16	8,575

the Haskell Ranch. Nero (1956b) reported the average size of 17 territories in Wisconsin to be 3,550 sq ft. Average size, however, increased from 1947 to 1953 as the breeding population declined. Linford (1935) found much larger territories in Utah (average: 31,603 sq ft) but his birds gathered most of their food on the territories whereas Nero's birds did not.

There is thus a general correlation between the size of Redwing territories and the proportion of food obtained within the confines of the territory. However, it is doubtful whether food *per se* is the proximate factor by which territory size is regulated. The available evidence suggests that many bird species use features of vegetative physiognomy as their major cues in evaluating environmental suitability (Lack 1940), though the mechanisms by which

this is accomplished are unknown. That this is also the case with the Redwing is suggested by change in territory size in response to stage of vegetative succession (Martin 1960) and by the response to burning of the marshes. The exceptionally complete burn at the East Park Reservoir marsh in 1960 left large areas devoid of emergent vegetation until the new growth appeared. In these areas the Redwing territories were initially several times larger than in 1959, but as the vegetation grew, additional birds inserted themselves, and territories became smaller (Table 9) though never as small as in the previous year.

TABLE 9. Size of Red-winged Blackbird territories on burned marshes, East Park Reservoir, 1960.

Roadside study area	Number of territories	Average size (sq. ft.)
April 29.....	3	26,500
May 15.....	4	19,875
North study area		
April 29.....	2	32,300
May 15.....	4	16,150

Food for the young may be gathered either on the territory or adjacent to it. The cattail areas at the south end of the main marsh at the East Park Reservoir were surrounded with sedge meadows from which much of the food was gathered, but often the birds flew across the road to an alfalfa field. Much food was gathered within the territory among centrally located territories. Where oak parkland adjoined the marsh, the birds frequently foraged among the grass and trees.

Several types of evidence suggest that territorial behavior is limiting breeding density on the study areas. Firstly, territorial challenges by newly arriving males are common much of the breeding season, and they may be vigorous and prolonged. For example, on April 19, 1959, I watched an intruding male, easily identified by his more orange epaulets, attempting to take over a territory for more than an hour. When first discovered at 0730, the intruder was submissive to the resident male, but by 0745 he began to give full song spreads on perches and in flight over the territory and began diving at the resident male, each time evoking a chase. By 0800 he was at times flying over the territory unchallenged by the resident, and his attacks were intensified so that he hit the resident while diving. By 0824 he was displaying to females flying over the territory, and had apparently succeeded in taking over, but at 0836 the resident male became more vigorous in his defense of the territory and the intruder left. He returned again at 0842 but was immediately chased by the resident and left again. By 0900 I had seen no further sign of him nor did he reappear later.

On April 30 at one of the isolated cattail patches I observed another unsuccessful territorial challenge which lasted intermittently from 1330 to 1445. The

challenger held a nearby territory without cattails or other emergent vegetation which could support a nest. These are extreme cases, but the frequency of occurrence of territorial challenging by both sexes suggests that more birds would settle if they could. Nero (1956b) has reported at length on this aspect of territoriality in Wisconsin Redwings.

A second line of evidence is provided by the behavior of birds which have been trapped and banded. Twice, males which I had trapped fought to regain their territories from new males even though the duration of their confinement could not have been longer than a few hours. Nero (1956b) reported this also.

To test the matter further, the males from an area at the East Park Reservoir, containing 7 territories, were shot on May 8, leaving only one color-banded male whose vocalizations were being studied. The following morning, this male and a bird from across the stream had expanded their territories to include most of the vacated area, and though this was late in the season, there were five replacements by May 17 (Fig. 11). Since this was later in the season than any new areas were occupied in this region, it is likely

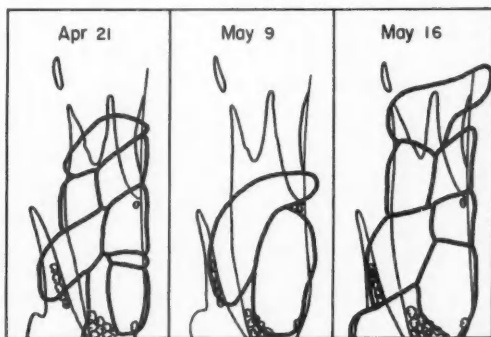


FIG. 11. Repopulation of a small marsh by male Redwings following shooting of the established territorial males. East Park Reservoir, 1959.

that the invading individuals were birds which had been prevented from breeding by the prior occupation of all territories by other males.

On the basis of these preliminary results, the experiments were continued in 1960. A section of the Haskell Ranch marsh and another area at the East Park Reservoir were selected as removal sites. Males were removed from the Haskell Ranch marsh eight times and from the East Park Reservoir five times (Table 10). At both sites first-year males, which do not normally hold territories, did so as removals continued. All such birds had functional testes. How long they would have been able to defend their territories successfully is not known. One of the replacement adult males, on the other hand, had non-functional testes.

Observations following shooting demonstrated that replacement was often quite rapid. Dr. Leopold observed the Haskell Ranch area on the morning of April 12, the day following the first shooting, and

TABLE 10. Red-winged Blackbird removal experiments, 1960.

HASKELL RANCH		EAST PARK RESERVOIR	
Date	Number of ♂♂ shot*	Date	Number of ♂♂ shot
April 11	5	April 11	2
April 20	5	April 28	3
April 23	3	May 7	3 (1)
April 28	2 (1)	May 15	3 (1)
May 8	3	June 8	2
May 15	3 (1)		
May 30	3 (1)		
June 16	2		

* Figures in parentheses indicate first-year males.

found all territories reoccupied. Several times I observed a replacement to occur within an hour and once within fifteen minutes. Particularly during April, when activity is at its peak, it would probably be possible to get daily replacement, so that the removals actually made give no idea of the number of birds which could be taken from a marsh during a season, nor what the seasonal pattern of time required for replacement might be.

Ever since the publication of Howard's (1920) book, territoriality has attracted considerable attention, but progress has not been commensurate with the effort expended (Hinde 1956). Data from blackbirds suggest some new avenues of approach. The role of territorial behavior in limiting the density of breeding birds, strongly indicated for the Redwing, should be tested for more species. Howard believed that density was limited by territorial behavior, but his view has been challenged by Lack (1954). Stewart & Aldrich (1951) and Hensley & Cope (1951) observed repopulation following shooting in coniferous forest insectivorous birds, but their experiments were performed during a spruce budworm outbreak and the results may not be generalizable.

The role of different factors in influencing territory size may profitably be explored by studying variability in territory size in different habitats. Some species, such as the Redwing, change their spacing system with habitat, providing clues to its significance. The value of comparative studies of closely related species has been largely ignored, but often such species differ strikingly in their territorial behavior. This aspect of blackbird spacing will be discussed following the presentation of data on the Tricolored Blackbird.

Mating System. It is well known that the Redwing is polygynous, the females maintaining territories within the larger territories of the males. Females regularly breed when they are one year old though it is not known if they always do so. Males do not normally breed until two years of age, though they have been observed holding territories (Beer & Tibbits 1950) and, rarely, breeding (Wright & Wright 1944, Nero 1956b) when one year old. First-year males, some of them reproductively ma-

ture, were common around the marshes and attempted to occupy territories. Some held small areas for short periods of time, but I had no evidence that they ever succeeded in fertilizing any females, nor is it known whether any of the first-year males which held territories after removals copulated with females.

Determining the number of males on a given marsh is a relatively simple task, but females are much more difficult to count. Counting all the nests in the area only gives a rough estimate of the number of females because of the many repeat nests following failure. Consequently, I was able to determine the actual sex ratios in only a small portion of the Redwings I studied. Precise figures are also rare in the literature. On my study areas the number of females per male has ranged from one to six. My data and those from the literature are given in Table 11.

TABLE 11. Red-winged Blackbird sex ratios.

Source	Number of ♂♂	Number of ♀♀	Average number ♀♀:♂
Smith (1943)	23	37	1.61
"	40	110	2.75
"	42-46	115-117	2.50-2.78
Nero (1956)	25	49	1.96
This study:			
E. Pk. Res.	29	108	3.72
Haskell R.	13	37	2.84

They suggest the possibility of geographical variation in sex ratio, but in the absence of data on temporal variation nothing definite can be said.

Male Redwings take no part in nest building or incubation. Most of them do not feed the nestlings either, but I observed one male at the Haskell Ranch and one at the East Park Reservoir regularly bringing food to the nestlings. Also, one male on Brooks Island was seen with food in his bill. Once the young fledge, however, the males regularly feed them.

Clutch Size and Nesting Success. Reliable information on clutch size is available only for 1960 (Table 12). No clutches of five or six were found at the East Park Reservoir in 1959, a drier year, suggesting that there might be some yearly variation in clutch size, but more data are needed to confirm this. Nesting success was also better in the wetter spring of 1960 (Table 13).

Feeding Behavior of Adults. During the breeding season, adult Redwings and Tricolors utilize a wide variety of animal and vegetable foods. The use of the bill in gaping in almost all feeding situations makes it possible for these birds to utilize effectively food resources unavailable to species which do not gape (Beecher 1951). Gaping appeared in my hand-reared Tricolors by the time they were two weeks old. The effectiveness of gaping is most striking when the birds are feeding in shallow streams. I have observed Redwings turning over stones weighing as much as

TABLE 12. Clutch-size in the Red-winged Blackbird.

Location	Year	NO. OF EGGS PER CLUTCH					Mean clutch size
		2	3	4	5	6	
Haskell Ranch.....	1960	1	9	10	—	—	3.45
E. Park Reservoir....	1960	2	23	55	4	1	3.75

TABLE 13. Fledging success of Red-winged Blackbirds, East Park Reservoir.*

Year	Number of nests	Average number of young per nest
1959.....	16	2.31
1960.....	12	3.00

* Note: Estimates based upon nests fledging at least one nestling; nestling counted as fledged if it reached at least an age of one week.

45 grams either by inserting the bill underneath the stone and gaping it up and away from the body with the upper mandible, or by pushing it toward the body with the lower mandible. This exposes the plecopteran and dipteran larvae beneath the rocks. Excrement of grazing animals is similarly handled.

Floating debris among stones and aquatic vegetation is frequently moved by a sideways motion of the head with the bill fully gaped. This same movement is also used when feeding in grassland where it is used to move dead material from the ground surface. It has also been reported to be used to extract spittle bugs from their froth (Macklin 1958). Regular gaping movements are also used in cattails and in grassland, the bill being inserted into the vegetation and then gaped to expose any insects and seeds within. Gaping is also used when the adults are feeding among the foliage of trees, but much foliage gleaning is achieved by merely searching from leaf clump to leaf clump without any gaping movements, and the same holds true for grassland feeding. Redwings have been reported splitting open dead ragweed stalks in the winter, thereby exposing pupae of *Epiblema strenuata* (Fischer 1953). In all gapers the skull morphology is modified to permit them to see straight ahead between the widely spread mandibles (Lorenz 1949).

In calm weather, the adults, especially the males, successfully catch insects on the wing, though they are definitely less adept than flycatchers or waxwings. On warm April and May mornings at Jewel Lake, when emerging dragonflies ascended from the cattails in their first flights, male Redwings were able to catch a large percentage of them, but if the bird missed on its first try, the insect was subsequently able to outmaneuver it, although waxwings still readily caught them at this stage. Both Redwings and Yellow-headed blackbirds utilize emerging dragonflies heavily in other areas also (Kennedy 1950).

In Californian annual grassland, filarees (*Erodium botrys* and *E. cicutarium*) are among the most

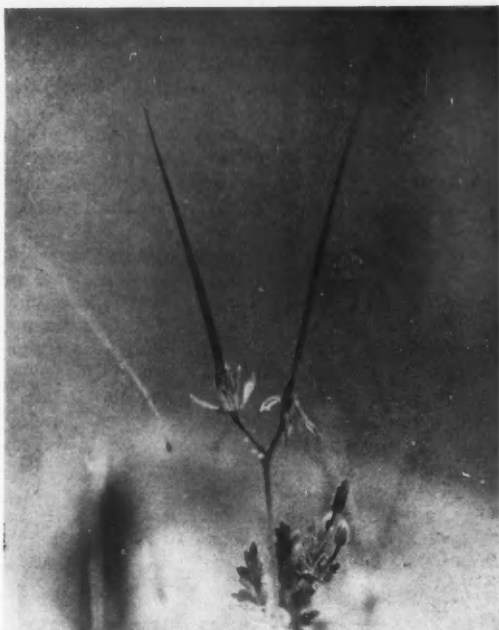


Fig. 12. Stripping of *Erodium* seeds by Redwings; seed on the right has been stripped.

abundant plants. When the seeds ripened in mid-April at the East Park Reservoir, the Redwings stripped the plants (Fig. 12), attacking the seeds from the base and peeling them off. In 1959, nearly all *Erodium* plants around the reservoir had been completely stripped by early May.

2. THE TRICOLORED BLACKBIRD

Non-breeding Period. Outside the breeding season, Tricolored Blackbirds feed in the same situations as Redwings and mixed flocks are common. Roosts are located in the same types of habitat and are often shared between the two species. Tricolors roost later in the evening than Redwings, and, in my experience, the sexes do not segregate at any time. As in the Redwing, there is a mass exodus from the Sacramento Valley in the late winter, birds being absent from large areas for several months. Since the Tricolor is not known to occur in large numbers outside the Great Valley of California, it is likely that the bulk of the population moves to the San Joaquin Valley where personnel of the U. S. Public Health Service, working on encephalitis control, observe them in enormous numbers.

Initiation of Breeding. The Tricolored Blackbird has long been known to be highly colonial when breeding (Heermann 1853, Mailliard 1900, 1914, Tyler 1907, Dawson 1923, Neff 1937, Lack & Emlen 1939), but little was known about the organization and operation of these colonies. In particular, no one had seen the events leading up to and culminating in the starting of a colony, nor had individuals been observed closely from blinds. It was one of the ma-

major objectives of this study to find out as much as possible about the organization of the breeding colonies of this species. I obtained detailed observations at the East Park Reservoir in 1959, and at the Haskell Ranch in 1960.

There is no other marsh within 30 miles of the East Park Reservoir, so that birds are forced to roost close to where they will nest. By mid-February, 1959, the reservoir had filled enough to reflood the marshes and several thousand Tricolored Blackbirds were roosting there. During mid-March some of the males began to display and preliminary exploration of cattails began. Birds flew to the cattails, sang, preened, and then suddenly shifted position and repeated the performance. From an observation tower erected April 5, however, I could clearly tell that while most males sang, few displayed. On April 15 only five or six males out of several hundred showed any signs of territorial behavior, and I had seen only one nest-invitation display.

The birds came to roost progressively later (Fig. 13) following the time of sunset, but after the first week of April they began to arrive earlier in the evening and spent more time singing in the cattails in the morning (Fig. 14). However, most of the

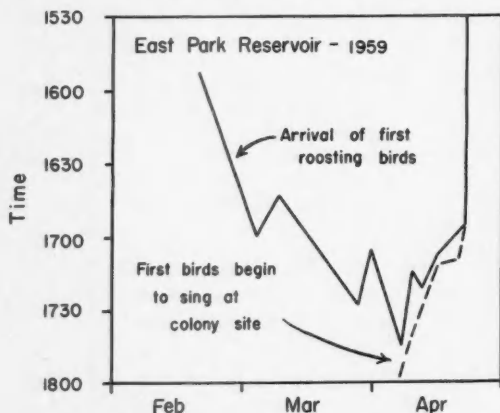


FIG. 13. Roosting of Tricolored Blackbirds, East Park Reservoir, 1959.

day was still spent, and most food was gathered, 10-15 miles from the roosting area.

Dense concentrations of flocks of birds at different loci in the marsh, first observed April 10, was quite conspicuous the subsequent week. Suddenly all the resting birds would fly up and gather in one spot, some of them landing, others fluttering above the vegetation. After a few minutes they dispersed again, only to repeat the performance at another spot a few minutes later. This continued through the first few days of colony establishment, and was noted at several other colonies during the nest-building period. At no time was I able to detect any change in the environment which might have triggered such behavior, and the latter may simply be a part of a colony-site investigation ritual.

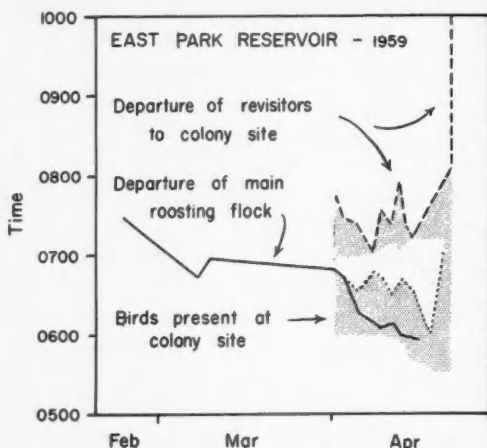


FIG. 14. Initiation of breeding among Tricolored Blackbirds at the East Park Reservoir, 1959.

Early in the morning of April 12, I first observed females carrying nesting material in their bills for a few minutes before dropping it. They were observed to do this again on April 14 and April 16, but it was not seen thereafter until true nest building started. In fact, evening activity of Tricolors around the marsh was generally reduced from April 16 to April 19, giving no sign of impending events.

On April 20 the birds remained all day. Hundreds constantly streamed back and forth from the cattails to the grassland feeding areas surrounding the reservoir. Displaying birds in the cattails shifted sites, formed dense concentrations, flew off to feed and returned. At times the whole marsh was deserted, all birds being scattered on the adjacent hill-sides, and then a few minutes later hundreds would stream back into the cattails. At 1300 I observed the first females carrying nesting material and early the next morning many were building vigorously. Though many birds immediately settled on territories others shifted from place to place in the cattails through most of April 22, but by April 21 most of the males were singing from platforms of bent cattails low in the vegetation. Often loud choruses came from a seemingly empty marsh.

By morning of April 22 nest building was intense in all areas which I could observe closely, and I saw the first copulation at 10:30. By afternoon copulations were occurring everywhere and many nests were already being lined. Both nest building and copulations continued all the next day and in the morning of April 24 I found the first eggs. By April 28 nest building was nearly over, but copulations continued everywhere. Many females were then incubating clutches of three eggs. By April 29 the males had nearly deserted the marsh and I saw only two females still carrying nesting material. I saw the last copulation April 30, after which there was no activity other than the feeding flights of incubating

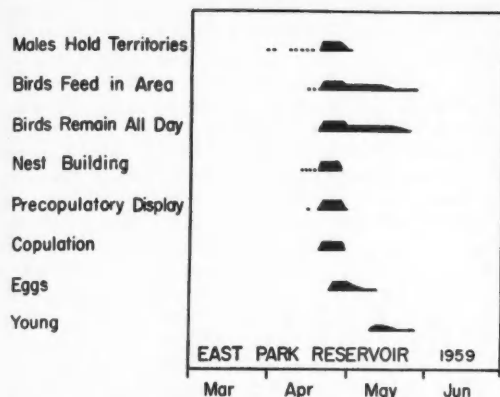


FIG. 15. Breeding chronology of Tricolored Blackbirds, East Park Reservoir, 1959.

females. The major features of timing of events in this colony are shown in Fig. 15.

In many areas in the valley Tricoloreds do not roost at the site prior to colony establishment. At the Haskell Ranch in 1960, small flocks occasionally flew over the marsh, but no birds were roosting in the breeding marsh as late as April 11. Nonetheless, thousands of birds were building nests April 19. Other observers have noticed active colonies in areas which were devoid of birds a few days earlier (Neff 1937), although in most cases early morning activity would not have been noticed.

Nesting Habitat. In addition to cattails and other emergent vegetation, Tricolored colonies are situated in a number of other vegetation types. Of the twenty-five colonies I have studied, 16 have been in cattails and other emergent vegetation, four in grain fields, one in alfalfa, one in a mustard patch, one in a safflower field, one in thistles along an irrigation ditch, and one in trees along a river. Of 236 colonies found by Neff (1937), mostly in the Sacramento and San Joaquin valleys, from 1932 through 1936, 224 were in cattails or other emergent vegetation. These differences may result, at least in part, from differences in searching habits of the different observers, but in most areas draining has been much more complete than it was when Neff made his studies. The favorable rice-growing areas are now virtually devoid of marshes, so that there is reason to regard at least some of the difference as real.

Time of Breeding. Extreme synchrony, as found at the East Park Reservoir, is characteristic of most colonies of Tricolored Blackbirds (Tables 14 and 15). Even in colonies as large as 50,000 to 100,000 nests, all eggs may be laid within one week. The number of nests started daily in a large colony (Haskell Ranch) and a small colony (Lake Isabella) are shown in Figs. 16 and 17. On the other hand, some colonies, such as the one at the Capitol Outing Club in 1959 and 1960, grow through the addition of new birds on their peripheries so that, while any given area is uniform, different parts of the colony vary. For example, at the Capitol Outing Club on June 5, 1959, young were being fed in nests in the northeast

TABLE 14. Time of events in Tricolored Blackbird colonies—Spring 1959.

Colony	Number of nests	Nest-building	Egg-laying	Incubation	Feeding young
E. Park Res.	1,500	Apr. 21-Apr. 28	Apr. 25-May 1	Apr. 28-May 11	May 10-May 20
Haskell Ranch	15,000	Apr. 28-May 6	Apr. 30-May 9	May 2-May 22	May 14-June 5
Mustard Patch	14,000	May 1-May 8	May 5-May 12	May 7-May 25	May 19-June 10
Marysville	40,000	May 3-May 10	May 6-May 13	May 8-May 31	May 20-June 14
Cap. Outing C.	80,000	May 8-June 9	May 11-June 12	May 14-June 16	May 28-June 28
Alfalfa Field	50,000	May 9-May 15	May 13-May 18	May 16-May 30	May 28-June 15
County Line	75,000	May 15-May 21	May 18-May 24	May 20-June 6	June 3-June 20

TABLE 15. Time of events in Tricolored Blackbird colonies, 1960.

Colony	Number of nests	Nest-building	Egg-laying	Incubation	Feeding young
Haskell Ranch-A	1,500	Apr. 18-Apr. 23	Apr. 22-Apr. 25	Apr. 25-?	destroyed
E. Park Res.-A	50	Apr. 21-Apr. 25	Apr. 25-Apr. 29	Apr. 28-May 9	May 7-May 29
Marysville	800	Apr. 29-May 4	May 2-May 6	May 5-?	destroyed
Madison	70,000	May 4-June 13	May 8-June 17	May 11-June 29	May 22-July 13
Buttes	6,000	May 10-May 15	May 14-May 19	May 17-?	destroyed
Gridley	35,000	May 11-June 14	May 15-June 17	May 18-June 28	May 30-July 15
County Line	4,000	May 17-May 25	May 20-May 29	May 23-June 9	June 2-June 30
E. Park Res.-B	600	May 17-May 22	May 21-May 25	May 24-June 6	destroyed
Riego Road-A	500	May 17-June 3	May 21-June 7	May 24-June 18	June 4-July 5
Cap. Outing C.	100,000	May 17-June 16	May 21-June 19	May 24-June 25	June 5-July 10
Haskell Ranch-B	15,000	May 23-June 25	May 27-June 29	May 30-July 11	June 10-July 28
Safflower	20,000	May 28-June 1	June 1-June 5	June 4-June 16	June 15-July 3
Riego Road-B	30,000	May 28-June 1	June 1-June 6	June 4-June 17	June 15-July 4

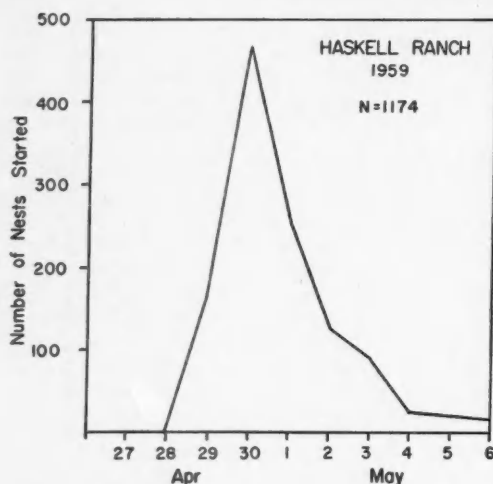


FIG. 16. Breeding synchrony in a large colony of Tricolored Blackbirds.

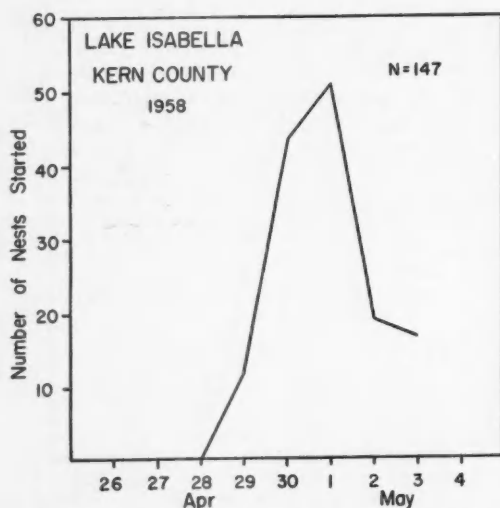


FIG. 17. Breeding synchrony in a small colony of Tricolored Blackbirds.

part of the colony, farther southwest all females were incubating, and at the extreme corner of the colony nests were still being constructed. This type of colony organization has been noted before (Tyler 1907, Dawson 1923, Lack & Emlen 1939), and Dr. Leopold has observed it in previous years at the Haskell Ranch.

Occasionally shortage of nest sites forces still a third form of synchrony not heretofore reported. In a colony found May 4, 1958, in Kern County, nests with eggs, others with nestlings, and still others with fledged young were mixed throughout the colony situated in a small patch of cattails growing in a stock-watering pond, which was the only marsh for miles. Apparently successive waves of birds moved

into the cattails to establish territories as soon as the preceding males vacated theirs. Two waves of birds established themselves in the Madison colony in 1960, and nests in all stages of construction and occupation characterized the two autumnal colonies studied in 1959 (Orians 1960).

Time of breeding varies considerably within small areas. Starting dates in colonies I have observed have ranged from April 1 to May 28, and eggs have been reported in the literature from April 1 to June 17 (Bent 1958). Basically, three major types of areas are utilized for breeding; the grazing lands and dry farming areas of the foothills, irrigated agricultural areas in the valley with little or no rice, and the rice-growing areas. In both 1959 and 1960, breeding began earliest in the foothills and latest in the rice country (Table 16) even when one includes the nesting at the East Park Reservoir in 1960, which was greatly delayed by burning. Early breeding in the foothills, also reported by Dickey & van Rossem (1922), occurs in spite of the fact that spring temperatures are cooler in the foothills than in the valley. It is adaptive because in non-irrigated country the vegetation dries up in May with the termination of the rains. However, before planting time in late April, the rice fields are dry and barren. After being reworked and fertilized, they are flooded with about eight inches of water and seeded from the air. To discourage other grasses from invading, the water is maintained at this depth until the rice has sprouted some 18 days later. When this occurs, the water level

TABLE 16. Time of breeding in the Tricolored Blackbird.

Year	Habitat	Number of colonies	Range of starting dates	Mean starting date
1958.....	Foothills	5	Apr. 1-Apr. 30	Apr. 20
1959.....	Foothills	1	April 21	Apr. 21
1960.....	Foothills	2	Apr. 21-May 17	May 4
1959.....	Valley cropland (no rice)	2	Apr. 28-May 3	May 1
1960.....	Valley cropland	4	Apr. 18-May 23	May 6
1959.....	Rice country	4	May 1-May 15	May 8
1960.....	Rice country	7	May 10-May 28	May 17

is lowered until only 1-2 inches remain. At this time adult blackbirds are able to wade through the shallow water or hop from clod to clod, gathering the insects which by then are becoming more common. Before this time the rice fields could not support Tricolor colonies.

Territory. Territory sizes in dense Tricolor colonies are difficult to measure accurately, but by estimating distances between neighboring males I have determined that territories are usually 35 sq ft or less in dense vegetation although they may be larger in less suitable cover. The area is defended without aerial displays from a low platform of bent cattails. The tops of the vegetation form neutral ground over which prospecting males and females move without being attacked. It is only when an intruding male actually moves lower down into

the vegetation that he is chased. The male defends his territory only for that week when the females are nest building and actively soliciting copulation. Once the clutches are complete he leaves and may not visit the territory again until the young hatch.

To support the food needs of thousands of young birds, a large area must be exploited by the adults and this area forms the ecologically significant territory. Figs. 18 and 19 show the pattern of utilization around the East Park Reservoir and the Marysville and Colusa colonies in 1959. At these colonies, birds travelled up to 4 miles from the colony site and more than 30 sq mi of land were exploited for food. At the Marysville colony, conditions were excellent for observing changes in feeding pattern during the nesting period.

Details of the temporal pattern of environmental utilization are given in the thesis manuscript deposited in the library of the University of California. The general picture which emerges from these observations is that Tricolors react quickly to any changes in the surrounding environment which make food supplies more readily available. As soon as pastures were flooded or a crop cut or raked, thousands of birds descended upon the newly exposed insect supply. The source of food is apparently communicated to others by the direction from which incoming birds approach the colony. I observed no spe-

● Colony site ■ Heavy Use ▨ Light Use

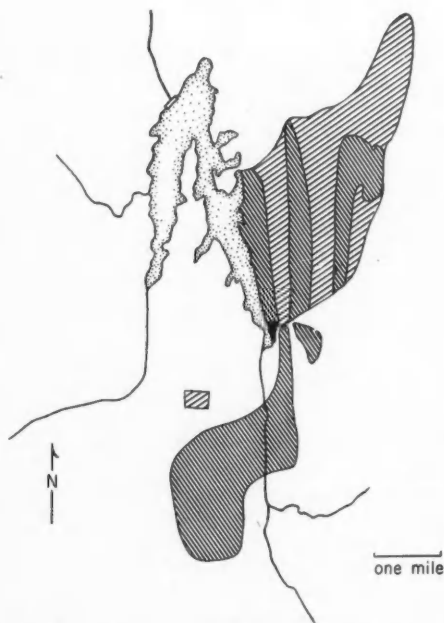
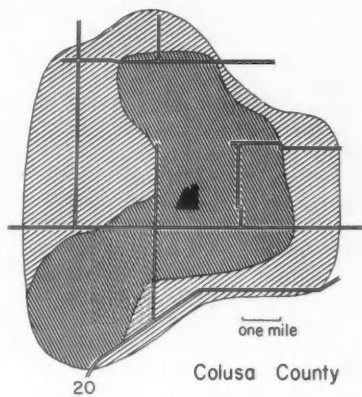


FIG. 18. Feeding grounds of Tricolored Blackbirds during nest building and incubation periods at the East Park Reservoir, 1959.



■ Colony Site ■ Heavy Use ▨ Light Use

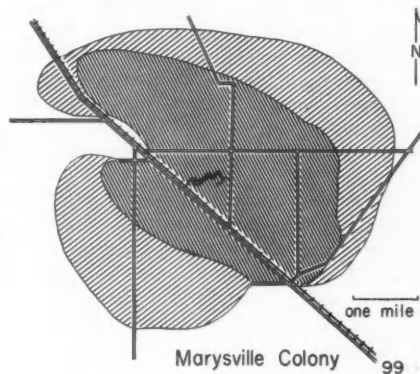


FIG. 19. Feeding grounds of Tricolored Blackbirds at the Colusa and Marysville colonies, 1959.

cial behavior which might have assisted with this, but communication was nonetheless efficient.

Mating System. As in the Redwing, the males do not breed until their second year, but at least some females do so when they are one year old. Two females banded as nestlings at the East Park Reservoir in 1958 were among the breeders in 1959. Yearling males regularly establish territories in the breeding colonies, but they are crowded into the less desirable sites. At the Haskell Ranch in 1960, three yearling males defended territories for several days around my observation blind. They gave the full complement of reproductive displays and vocalizations, and successfully evicted prospecting adult males. One of the yearlings attracted a female that started building a nest, but she stopped when it was half completed. I saw no first-year males copulating with females, but cannot assert that they never do. In contrast, Lack & Emlen (1939) reported that first-year males did not hold territories but rather dashed in for attempted copulations. Since I did not observe first-year males

holding territories until I watched closely from blinds erected within the colonies, perhaps their failure to see this is a byproduct of their observing from a distance.

Sex ratios are difficult to determine accurately in dense colonies, but my observations and those of Gerald Collier suggest that normally there are only two females per male, rarely more. In many cases there is only one nest constructed in an area defended by one male. To determine the breeding sex ratio requires hundreds of marked birds, something which no one has yet achieved. Lack & Emlen (1939) closely observed three males, one of which had two females, the other two had three, but little can be said from such a small sample. They also estimated a ratio of 47 ♂♂:100 ♀♀ in birds coming in to feed the young. Even assuming this estimate was accurate, it cannot be interpreted definitely until the relative feeding rates of males and females are known. Estimates are also complicated by the presence, for short periods of time, of more females within the territory of one male than actually complete nests. The mechanisms by which the sex ratio in a colony is determined are unknown. Females are not aggressive toward each other as female Redwings are, but the possibility of subtle behavioral interactions between females cannot be excluded because they do have a special call which is given when approaching and leaving the nest.

Nests are built by the females only. Although males often manipulate nest material in nest-site demonstration displays, I have only once seen a male carry nest material any distance. The nest normally is completed in four days or less. Materials used are similar to those utilized by the Redwing but Tricoloreds usually line the nest with green grass while Redwings use dry grass. Most of the material for the nest is gathered on the marsh, but at the lining stage the females may travel for some distance to a good grassy area to gather the fine green lining material.

Incubation is performed by the females alone. The males leave the marsh during the day at this time, returning at night to roost, but not necessarily roosting on their territories or even within the confines of the colony. Incubation takes 11-12 days (Emlen 1941. Confirmed by my studies). During the incubation period, the females take long feeding flights several times each day, there always being a mass exodus the first thing in the morning and then again late in the afternoon. At the East Park Reservoir on May 1, 1959, there was a mass exodus of females at 0515, the first birds returning at 0607. During the rest of the day small groups regularly flew back and forth from the marsh to the feeding areas. In the afternoon I watched a flock of 200-300 feeding in chamise about one mile northeast of the colony. The flock remained approximately the same size for over an hour but during that time its membership changed several times as new birds joined the flock and others left it and returned to their nests. The unity of the

feeding group was maintained because outgoing birds followed the paths of returning birds.

Clutch Size. Estimates of clutch size may easily be made by walking through the colony during the incubation period. Because of inevitable losses prior to the time of counting, such estimates represent the minimum clutch size. For example, Paynter (1941) found an average clutch size of 2.38 in the Herring Gull (*Larus argentatus*) whereas histologic examination of the ovaries shows that invariably three eggs are ovulated (Davis 1942). During this study I made clutch size determinations at six colonies. Omitting rare clutches of 1, which are almost certainly incomplete, estimates ranged from 3.01 to 3.44 (Table 17). It is of interest that all three 1960 determinations are larger than the 1959 ones. Emlen (1941) found a mean clutch size of 3.6 eggs in 141 nests, a

TABLE 17. Clutch-size in the Tricolored Blackbird.*

Locality	Date	NO. OF EGGS PER CLUTCH					Mean clutch size
		2	3	4	5	6	
North Colony, E. Park Res.	4/29/59	5	34	23	—	—	3.29
Main Colony, E. Park Res.	5/ 2/59	32	99	34	—	—	3.01
Main Colony, E. Park Res.	5/29/60	12	93	97	2	—	3.44
Haskell Ranch	5/13/59	164	715	259	2	1	3.09
Haskell Ranch	4/27/60	13	77	56	—	—	3.33
Marysville	5/20/59	56	147	89	—	—	3.11
Marysville	5/ 8/60	7	78	74	—	—	3.42

* Note: rare clutches of 1 are omitted.

value larger than any I found, but the data are not sufficient to establish annual variations in clutch size. Autumnal clutch size was similar to that of spring (Orians 1960). Clutches of 5 or more may represent contributions from more than one female, but they are so infrequent that they do not appreciably influence mean values.

Nesting Success. During my studies I have observed nest failures of three main types. At the Marysville colony on May 30, 1959, when the oldest young were about 10 days old, I visited hundreds of nests. In only three nests were there three young older than one week, and in each of these nests one of the nestlings was considerably smaller than the other two. Even in nests with only two young one week old or older, one was normally a runt. There were hundreds of dead young beneath the nests. Neff (1937) also reported the death of many of the smallest of the nestlings, finding that this percentage was greater later in the season than earlier. He attributed this to the great heat of the marshes in June which caused incubation to be therefore less synchronous. Since feeding conditions are probably poorer later in the season, the youngest nestlings might have died of starvation whether or not hatching was asynchronous. Starvation of nestlings was also widespread in the autumnal colonies (Orians 1960).

A second form of nest failure is desertion. At the East Park Reservoir in 1959, mass desertion began on May 2. At that time I found only 188 nests with warm eggs out of 491 nests checked. Two Scrub Jays (*Aphelocoma coerulescens*) were seen flying from the colony with eggs in their bills, but they could not have accounted for more than a fraction of the eggs destroyed and were most likely taking already deserted eggs. By May 7, there were no more than 15 active nests where there had been over 1,000 one week earlier. On May 15, only eight females were feeding young. Neff (1937) also noted a number of colonies which deserted full clutches of eggs with no obvious cause. He also noted desertions resulting from wind damage to the cattails. At the East Park Reservoir there was no such disturbance, and nests and eggs were intact when deserted. Mass desertion also occurs in other colonial species (Brown 1958).

The spring of 1959 was unusually dry. Less than one inch of rain fell in April and only a trace in May. Consequently, the growth of annual grasses around the reservoir was exceedingly poor, and by mid-April the hills were already turning brown. No measurements of insect populations were made but they were surely far below normal. Possibly the birds made an assessment of the food available in the surrounding feeding areas by means of the feeding flights to be described, and nesting was abandoned because of the inadequacy of the food resources. Mass desertion of full clutches also occurred in the autumnal colonies in 1959, where it again could be correlated with inadequate food supplies in the surrounding areas. The reasons for believing that an abundant and readily available food supply is especially critical for colonial species will be dealt with later.

A third form of nest failure is loss to predators. I have not witnessed nest destruction in this species, but several colonies have been destroyed within a few days. In 1959, a small colony at the East Park Reservoir north of the main marsh was destroyed at the same time the main colony deserted. On May 7 all the nests were intact but empty. In 1960 both the Haskell Ranch colony and the Marysville colony were destroyed. Bits of eggshell or yolk stains were found in some of the nests, but in most of them there was no sign of disturbance. Mass destruction of nests has also been reported by Mailliard (1900), Neff (1937) and Lack & Emlen (1939). Various predators have been accused, among them snakes, hawks, owls, crows, mink and raccoons. I have seen both Scrub Jays and Yellow-billed Magpies (*Pica nuttalli*) taking eggs from colonies, but the number of birds present could have taken but a small fraction of the eggs and young lost. It is more likely to have been snakes (*Thamnophis* and *Pituophis*), which are able to climb cattails to the nests, are common in the marshes at this time of year, and have been seen robbing Redwing nests.

Feeding Behavior of Adults. Food and feeding of adult Tricolors appears, without examination of

stomach contents, to be similar to that of the Redwing, but their social organization results in their feeding in different areas even when the two species are nesting in the same marsh. A flock of Tricolors feeding in a grassland or other uniform place progresses by the flight of the rear birds over the rest of the flock to the front. A given individual usually spends 25-40 seconds in one spot before flying to the front of the flock. Thus, the flock smoothly progresses across the ground even though its individual members move only twice per minute. In rice fields and flooded pastures no such uniform pattern of flock movement is possible and individuals move more at random with respect to each other.

Colony-size Limitation. Evidence has been presented for the Redwing indicating that territorial behavior limits the density of the breeding population. In the Tricolored Blackbird, territory size varies little from colony to colony unless the vegetation prevents the nests from being as close together as they normally are in undisturbed cattails. Furthermore, except in rare instances, the total nesting space is only partly utilized by the colony, so that territorial behavior would be ineffective in preventing additional birds from settling to breed. Nevertheless, when enormous numbers of individuals must be fed from a fixed spot, the relationship between colony size and food supply is critical because a colony too large for the surrounding environmental resources might be a complete failure. Certain evidence strongly indicates that there is some mechanism of colony-size adjustment, although its details are yet to be determined.

Firstly, colony size is correlated with the suitability of the surrounding environment. In the grazing lands of the foothills I have never found colonies larger than a few thousand nests. The agricultural country of the valley supports larger colonies, the largest being in the rice-growing areas where rich insect supplies are produced in the shallow water (Table 18).

TABLE 18. Tricolored Blackbird colony sizes.

Habitat type	NUMBER OF COLONIES WITH		
	<1,000 nests	1,000-10,000 nests	>10,000 nests
Foothills	7	2	1
Valley cropland (no rice) ..	3	2	3
Rice country	0	3	7

Secondly, territorial challenges are frequent during the colony-establishment period. Territories are often taken over by a new male while the resident is absent for a few minutes feeding, but such intruders are quickly expelled by the owners when they return. At any time during the colony-establishment period there are many unsettled birds which continually move back and forth over the colony looking for unoccupied territories. In fact, from a distance it appears that most birds are wandering aimlessly

through the colony area. Actually, the established males are all singing and displaying low in the vegetation, and the movements are almost entirely composed of unestablished birds. This is not correlated with availability of territory sites because it is equally true whether there is a shortage of nest sites or whether only a small portion of the marsh is occupied. Apparently intruders attempt only to substitute themselves for already established birds rather than to increase the colony size.

Thirdly, in all colonies observed at the time of territory establishment, the number of birds present was always greatly in excess of the number which actually remained to breed. At the East Park Reservoir in 1959, about twice as many birds were present the first few days as bred. At the Haskell Ranch in 1959, about three or four times as many birds as nested were present the first few days. Some of this overflow may have moved to the Marysville Colony about eight miles to the northeast, but even here the colony at its maximum extended nearly one-fourth mile farther along the drainage channel than the limit of actual nests. In none of these cases was there a shortage of nesting sites.

The evidence suggests that during the first few days of colony establishment an assessment is made of the food supply available in the surrounding environment by means of mass feeding flights. During this period the birds make what appears to be an excessive number of feeding trips to the surrounding country, and by watching from a blind it can be determined that unestablished birds make far more trips than established ones. These mass feeding flights form the most conspicuous activity around colonies at this time. At the East Park Reservoir in 1959, I observed 17 mass feeding flights, involving most of the birds in the colony, in 6.5 hrs on April 20, the day the colony started. On April 21 I observed 14 such flights in 4.75 hrs and on April 22, 5 in 2.25 hrs. This yields an average of 2.7 flights per hour. It seems unlikely that such a rate of feeding is necessary for the adults merely to gather the amount of food they need.

This is simply a special case of the general phenomenon of environmental evaluation among birds. Many species are known to adjust their clutch sizes and/or territory sizes to food supply of the environment, and it is well known that colony size in many colonial species is in some way adjusted to the capacities of the environment to support breeding (see references in Lack 1954). Such an adjustment could be made in the Tricolored Blackbird through the mass feeding flights.

Data for the Redwing and Tricolored Blackbird relative to spacing can be summarized as follows. In the Redwing, territorial behavior strongly limits density, forcing part of the population into less suitable areas and probably totally preventing some individuals from breeding. Fighting over territories begins early and is most severe in areas where territory size is ultimately the smallest. Variability is related to habitat in two ways: (1) The nature of

the nesting vegetation may influence territory size, as was shown following burning. Under undisturbed conditions, however, this is likely to be of minor importance. (2) More important is the nature of the surrounding feeding grounds. Territories are largest where most of the food is obtained on them and smallest where the least food is obtained on them. Territory size is unrelated to the number of females building nests within it, nor is it related to the action of known predators, though this point is less certain.

In the Tricolored Blackbird, territories are uniformly small unless the vegetation is not dense enough to permit such a high concentration of nests. Territorial behavior does not limit density. Instead, the important variable, colony size, changes with environmental conditions, being smallest in the grazing and dry farming areas and largest in the rice growing areas. There is suggestive evidence of a mechanism of colony size limitation.

Therefore, whereas in neither species is there a "food territory" in the classical sense, the spacing within the systems is intimately related to the exploitation of the environment, and the known patterns of variability in territory size can be attributed primarily to it. More data will be needed to clarify the roles of other factors.

TIME AND ENERGY BUDGETS

The amount of time and energy which a bird devotes to different activities must inevitably influence its survival and reproductive rates. It follows that there exists for a species in a given environment an optimal time and energy budget. It is of particular theoretical interest to investigate the conditions influential in determining the relative significance of different patterns of time and energy budgeting (Hutchinson 1957, Fisher 1958:47). The general evolutionary trend has been to reduce both the number of gametes produced and the amount of energy devoted to their production. At the same time there have been increases in the energy content per female gamete, and the time and energy devoted to the care of those few offspring produced. It is not surprising that these trends are correlated since giving extended care to offspring is incompatible with producing enormous numbers of them, and production of large gametes is incompatible with production of large numbers of them. Beyond these obvious trends, however, there are many unstudied variations in the time and energy budgets of species producing similar numbers of gametes of approximately equal energy contents.

There are three major ways in which a species can modify its expenditure of time and energy. Firstly, the total energy expenditure may remain approximately the same but its distribution among different activities varied. Secondly, the total energy budget may be increased, and thirdly, it may be decreased. The amount of time spent on reproductive activities may vary in like manner. It is the purpose of this section to present quantitative estimates of

time and energy expenditures in the Redwing and Tricolored Blackbird.

These estimates are of necessity rather crude. Firstly, the lack of adequate physiological data forces me to make assumptions about the energy demands of certain activities which may not be highly accurate. Secondly, the field data are based upon only a few individuals, whereas observations in other areas have shown that the pattern varies geographically. No previous attempt has been made to establish the budgeting of time and energy in natural populations, but Pearson (1954) made an estimate of the daily energy requirement of an Anna Hummingbird (*Calypte anna*). Hence, in spite of the various difficulties involved, crude attempts will nevertheless be ventured because the differences between the two species of blackbirds are so striking and because of their theoretical importance.

Ideally, one should present estimates of the entire annual time and energy budgets but the data do not justify such extended treatment and non-breeding differences appear to be minor. Instead, I have limited the comparison to those features in which the two species differ most strikingly, namely territorial defense and feeding of the young. The slight differences in the time and energy devoted to nest building and egg laying are ignored. These restrictions serve to concentrate attention upon the major differences, in terms of energetics, between the two social systems, preparing the way for a discussion of the evolution of these differences. Since no attempt is made to quantify the entire time and energy budget, it is impossible to express any time and energy expenditures as fractions of the whole. I have therefore expressed them as percentages of energy increase above the resting metabolic level, or as additional hours of time expenditure, as the case may be.

My most complete information on the Redwing is based upon several males studied intensively at Jewel Lake in 1958. During February the males spent about fifteen minutes on the marsh in the morning, defending their territories, after the departure of the main roosting flock. They then left for the day, returning in the evening shortly before the main roosting flock at which time they also engaged in territorial behavior. In March, the time spent on the marsh gradually increased to about 3.5 hrs in the morning, but the evening arrival time did not appreciably change. On the average, about two extra hours were spent on the territories during this month. By the end of the first week of April the birds remained all day and nesting was soon underway. This pattern continued for about two months until nesting was completed, after which the birds again left the area.

Once the males remained all day, about $\frac{3}{4}$ of their time was spent on the territory; the rest on nearby feeding grounds. From my notes I have determined that about $\frac{1}{4}$ of the time spent on the territory was occupied with actual defense of the territory, either by means of vocalizations and dis-

plays or through actual chasing and combat (see later).

As females are much more difficult to watch, I do not have comparable quantitative data, but they spend much less time in territory defense than males, and the period of time during which they do so is shorter. Territory defense at Jewel Lake lasted from mid-March until the hatching of the eggs, but during the incubation period the frequency of contacts between females was low as incubating birds stirred from their eggs only when new females arrived on the area. During the period of active territorial defense, I estimated that about $\frac{1}{8}$ of the female's time is so spent.

Once the young hatch, the pattern of activity suddenly changes for the females, but not for the males, which continue much as before. On the average, a female visits the nest at least once every fifteen minutes with food. Most of her time is spent among

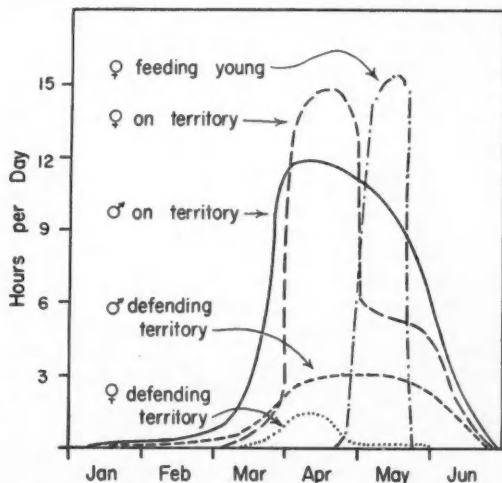


FIG. 20. Time and expenditure during the breeding season by a typical pair of Redwings.

the grass searching for food, only about 1.5% of it being required for flying to and from the nest. The remainder of time is devoted to feeding herself, preening, and resting. An estimate of the time expenditure of a typical male and female Redwing is summarized in Fig. 20.

In the Tricolored Blackbird, the pattern is strikingly different. Prior to the start of nesting almost no time is devoted to activities concerned with breeding, but activity is intense as soon as the colony forms. Since continued observations of individuals in these colonies is so difficult, estimates are based upon group behavior, supplemented by observations of individuals from a blind. Males devote about $\frac{1}{2}$ of their time to territory establishment and defense during that one week period when nests are built and eggs laid. Thereafter, such activity ceases for the remainder of the breeding period. Since nests are started the first day, females spend almost no

time in aggressive behavior. Once the eggs are laid, all territorial behavior on the part of all birds stops.

During the colony-establishment period considerable energy is devoted to the conspicuous mass feeding flights. About 26 minutes of every hour were devoted to feeding flights, a portion of which apparently forms a part of the environmental assessment of the breeding birds.

During the nestling period, both sexes actively bring food to the young, but in contrast to the Redwing, the major expenditure is in flying from the nest to the feeding area and back again. Since areas up to four miles from the nest are utilized when feeding the young, virtually half of the adults' time must be spent in flight, leaving much less time for gathering food than is available to the Redwing. If as much time were spent on foot by Tricolors, the rate at which food could be delivered would be greatly reduced, and the reproductive rate lower, although this is partially offset by male participation in feeding of the young. Since the clutch size of the Tricolor is only slightly less than that of the Redwing, it is apparent that searching time has been reduced substantially. An estimate of the time expenditure of a typical male and female Tricolor is given in Fig. 21.

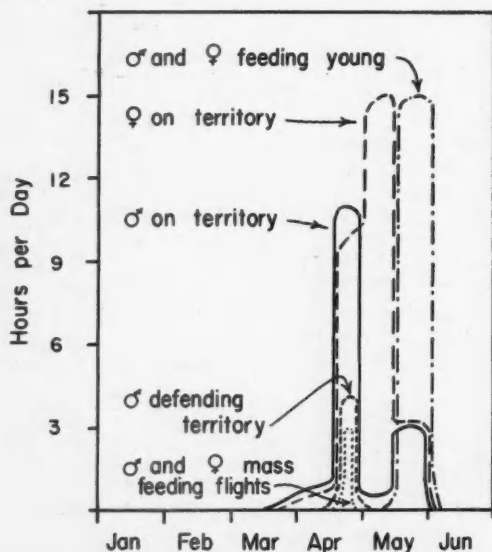


FIG. 21. Time expenditure during the breeding season by a typical pair of Tricolored Blackbirds.

Knowing the frequency of occurrence of different behavioral patterns during the nesting cycle, it is possible to calculate the energetic drain incurred by individuals of the two species. I am assuming that the physiology of avian protoplasm is similar to mammalian, an assumption supported by recent work of James R. King (pers. comm.). Estimates are based upon data given in Brody's book (1945) and Pearson's (1950) work on hummingbirds. Behavior

concerned with territorial defense may be divided into three categories: vocalizations, displays, and chasing and combat. The first two are energetically much more efficient means of accomplishing the objective and are consequently prominent in avian territorial behavior. For the purposes of calculation I assume that the energy required to produce song and other vocalizations raises the metabolic level of the bird 10 per cent above its resting level. This is equivalent to the additional energy required for standing as opposed to lying in man and several domestic animals (Brody 1945). Displays are assumed to double the metabolic rate much as walking does for man. Flight is assumed to require five times as much energy as resting, as found by Pearson for hummingbirds. Even if the flight of other birds is found to require an increase in energy less than that incurred by hummingbirds, the general picture obtained here will not be seriously altered.

Approximately six vocalizations per minute were given by male Redwings on their territories at Jewel Lake. Of these, five, mostly songs, were directly concerned with territory. Since the average duration of a song is slightly less than 1.5 seconds, about seven seconds per minute were devoted to this activity. Three displays concerned with territory were given per minute, averaging two seconds each, for a total of six seconds per minute. Flights and fights occupied about 1.5 seconds per minute. Thus, as mentioned earlier, $\frac{1}{4}$ of the bird's time is devoted to activities of territorial maintenance. Calorie-wise, the vocalizations require an increase of 0.7% in energy expenditure, the displays an increase of 5% and the flights and fights another increase of 5%, for a total increase of 10.7%. Furthermore, this 10.7% additional energy must be obtained in $\frac{3}{4}$ the time otherwise available for this purpose, and time available for other activities is correspondingly reduced. Since the male takes no part in feeding the young, his reproductive energy expense is restricted to this category until the young leave the nest.

In females the duration of territorial defense is only about one-half that of the males, and all forms of territorial behavior are indulged in less frequently, especially chasing and fighting. I have used an energy increase of 5% as an approximation of female territorial energy expenditure. However, once the young hatch, female time and energy expenditure changes radically. Assuming that walking on foot searching for food doubles the metabolic rate of the bird, the energy increase of females is about 157.5% above the resting level, about 150% of this coming via the search on foot and the remainder in flight between the nest and the nearby feeding grounds (Fig. 22).

In the Tricolor, the energy devoted to territorial defense and maintenance is greatly reduced in both sexes. All such activity takes place within the period of one week, and no energy is devoted to it during the incubation and nestling periods by either sex. Using mass behavior observations I have estimated that for one week, male Tricolors are at least twice as active

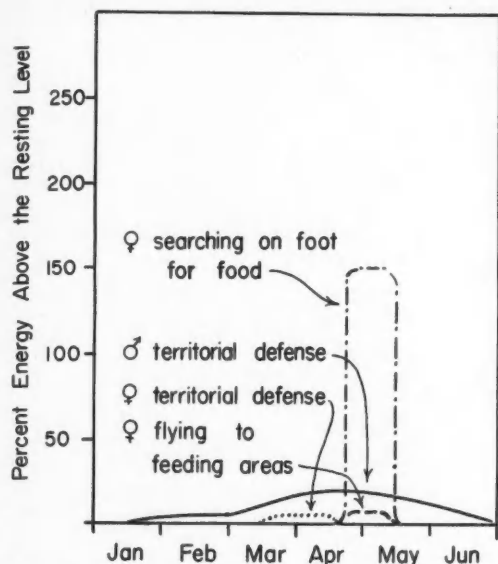


FIG. 22. Energy expenditure during the breeding season by a typical pair of Redwings.

in territorial defense as male Redwings, but that females are much less so than female Redwings. To this estimate must be added the energy expense of mass feeding flights, one half of which will be assumed to be in excess of that merely needed to sustain the adults.

The major energy expenditure accompanies feeding the young because of the great distances flown. Using the calculations of time spent flying and walking given in Fig. 21, it can be concluded that the energy increase totals about 317%, 250% of which is expended in flying and 67% in walking, just the reverse of that found in the Redwing. The other contrast is that both sexes are involved. Energy expenditure is estimated in Fig. 23 for a typical male and female.

In determining the total energy requirements of a social system it is important to consider not only the energy demands of the activity, but also the duration of that demand. In comparing the two systems I have therefore expressed the energy expenditure, firstly, in terms of the period during which it occurs and, secondly, in terms of the total energy increase for the year (Table 19).

Clearly the colonial system of the Tricolor is more demanding of energy but less demanding of time than the territorial system of the Redwing. This is due to the fact that most time-consuming events are energetically less demanding than events compacted into short periods of time. Since the colonial system of the Tricolor is energetically more expensive, the species would stabilize at a lower population level, other things being equal (Slobodkin 1953). However, it is probable that the system evolved because it made other things unequal, and that the population level

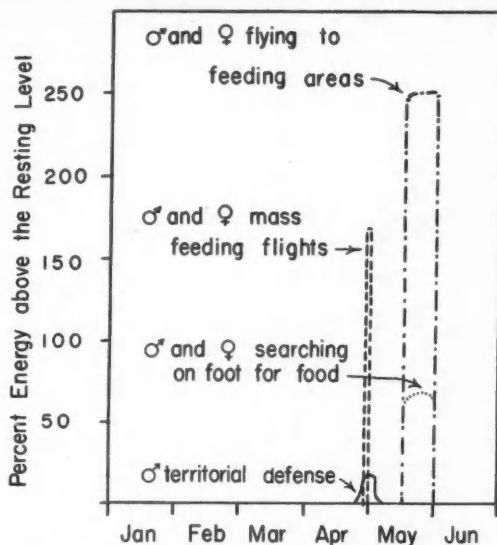


FIG. 23. Energy expenditure during the breeding season by a typical pair of Tricolored Blackbirds.

was increased by the adoption of the nomadic colonial system under the particular conditions to which it has been exposed during its history (see later).

Because of the high rate of food gathering, the Tricolor colonial system demands more favorable environmental conditions in which to operate than the Redwing territorial system. These more exacting requirements may help to explain the peculiarly spotty distribution of the species during the breeding season. A detailed study of food supplies available in different feeding areas, in relationship to their distance from the nests and the frequency of their utilization, would be most rewarding.

One of the major differences between the species is the early occupation of territories by male Redwings. Since testis maintenance is probably energetically cheap, only a very slight advantage for the males to be in reproductive condition early is needed to offset the energy loss incurred through the long-term maintenance of functional gonads. The advantages of early testis maturation are (a) early occupation of territories with the attendant advantages of prior residency, (b) the advantage gained by being able to mate with the first females to come into breeding condition (Fisher 1958), and (c) the ability to inseminate females whenever the opportunity arises. The relative importance of these factors varies with the particular mating system employed by the species and the ecology of the area. In many regions early occupancy of territories by the males is prevented by ecological unsuitability of the nesting area prior to the time of nesting.

In contrast, since the maturation of ovaries and the production of eggs is energetically very expensive, selection can be assumed to favor such metabolic exertion when and only when the chances for success-

TABLE 19. Comparative social system energy expenditure (expressed as % increase above the resting metabolic level).

Activity	REDWING						TRICOLORED BLACKBIRD					
	Duration		Energy increase %		Total energy increase %/yr.		Duration		Energy increase %		Total energy increase %/yr.	
	M	F	M	F	M	F	M	F	M	F	M	F
Territory defense.....	10 wks	5 wks	10.7	5.0	2.2	0.5	1 wk	1 wk	13.0	1.0	.25	.02
Mass feeding flights....	—	—	—	—	—	—	4 days	4 days	165	165	1.8	1.8
Feeding young.....	2 wks	2 wks	T	157.5	T	7.8	2 wks	2 wks	317	317	12.6	12.6
(flight to feeding area).	—	—	—	(7.5)	—	(0.3)	—	—	(250)	(250)	(10)	(10)
(search on foot).....	—	—	—	(150)	—	(7.5)	—	—	(67)	(67)	(2.6)	(2.6)
Total.....			10.7	162.5	2.2	8.3			330	318	14.65	14.42

Note: Duration of territory defense in the male Redwing may last up to 20 weeks but for part of this time the territory is occupied morning and evening only. The figure of 10 weeks represents an amount of time roughly equivalent to the total hours of full-time occupation.

ful breeding follow with a high probability. Furthermore, early breeding does not carry selective advantage for the female as it does for the male because the modal breeding time is necessarily the most advantageous if the breeding period is to stabilize, as it does. Hence, females are at a selective advantage if they come into breeding condition only upon arrival at a suitable breeding area where environmental conditions are favorable and a male is present. Thus, we should expect the female gonadal cycle to lag behind that of the male and the stimulatory effects of the male upon ovarian maturation to be strong, and this is the case.

Viewed in this light, the early occupation of territories by male Redwings in California, where winters are mild and the species is non-migratory, is reasonable, but male Tricoloreds fail to occupy territories prior to the time of breeding under the same environmental conditions. One of the requirements for adaptation to nomadism, the need for rapid response to suitable environmental conditions whenever and wherever they are encountered, leads to close group synchrony. Since the time and place of suitable breeding sites are unpredictable for nomads, no advantage can be gained through attempted occupation of sites in advance of the main group of birds. Instead, close flock organization at all times is most advantageous and the male's chances of leaving offspring are greatest if he remains with the group.

THE EVOLUTION OF MATING SYSTEMS

In most species of birds for which there is information, the sex ratio among nestlings is equal (Mayr 1939, Lack 1954:10), and there are important theoretical reasons for believing that the primary sex ratio should be close to 50:50. Fisher (1958) has argued that natural selection will tend to equalize parental expenditure devoted to the production of offspring of the two sexes, and Kolman (1960) has expanded the theory to show how this fixes the sex ratio but not the variance. As yet there has been no experimental confirmation of this hypothesis, but experiments with house mice are currently underway at the University of Pennsylvania. If, however, we

assume that Fisher is correct, there will be equal numbers of male and female blackbirds at the time they become independent of their parents, as found by Williams (1940). McIlhenny (1940), however, reported a sex ratio of 77% ♂♂ : 23% ♀♀ in Redwings from Louisiana, sexed at the age of five days in nests from which all young were known to have survived to the day of sexing. He did not state how he sexed the individuals, however, and Selander (1960) has since found that the sex ratio in Boat-tailed Grackles does not differ significantly from 50:50, though McIlhenny claimed to have found 30% males and 70% females. Selander concluded that McIlhenny sexed the nestlings on the basis of size only, and that his determinations are not trustworthy. Williams (1940) sexed 119 young Redwings, representing the full egg complements of 35 nests, finding 57 ♂♂ and 62 ♀♀. Among 94 young which successfully fledged the sex ratio was even. Hence, there are no reliable data which would suggest that the primary sex ratio in Redwings deviates significantly from equality, nor is there any reason to expect significant differences in the mortality rates of the two sexes during the nestling period. Once the adult plumage is attained, males might be expected to have higher mortality rates, but this does not influence the evolution of the primary sex ratio (Fisher 1958).

Unfortunately, there exist no satisfactory data on the sex ratio of adult Redwings or Tricoloreds. For much of the year sexes segregate in the Redwing, so that random field counts are worthless. Only at the time of breeding can the sex ratio be accurately determined, and this tells nothing about the sex ratio in the non-breeding segment of the population. Normally, the sex ratio among breeders has been assumed to be the same as in the population as a whole of breeding age but this is not likely to be true. The interesting data of Williams (1952) on the Brewer Blackbird demonstrate that this simple answer is insufficient.

It is well known that in many monogamous species occasional polygamous matings occur. Let us assume, then, that in many species there is a certain proportion of males having a genotype which makes it pos-

sible for them to have two mates. If, by having more than one mate, the male can produce more young than if he had just one mate, selection will always occur in favor of polygamy. Justin Frost has pointed out to me that the system is self-accelerating once it has started, so that once some polygamy has been established, fewer and fewer offspring are required per female mate from polygamous males to keep the selection going. This is true no matter how the mechanism is inherited and no matter what the sex ratio in the population as a whole. Thus, one can equally well ask why monogamy is so prevalent as why some species are polygamous. In view of this, and the theoretical likelihood of equal numbers of both sexes at the time of achieving independence, it is unnecessary to consider polygamy as the by-product of unbalanced sex ratios in the population as a whole, or as the by-product of a slower maturation rate of one sex.

In addition to the advantage conferred upon males having more than one mate, polygamy may be fostered by the advantage of having fewer males present on the breeding grounds to consume valuable resources (Pitelka 1959). In many species, particularly herbivorous mammals and precocial birds, the value of the male may be limited, if not non-existent, once fertilization has taken place. It is noteworthy that monogamy is rare among herbivorous mammals where the male is physiologically incapable of contributing to the nutrition of the young.

Counteracting this tendency toward promiscuity are other factors which must be operating in most species to maintain monogamy in the face of strong selective pressure against it. In species, such as carnivorous mammals and most birds, in which the male is able to make a significant contribution to the care of the offspring, a given male may not be able to leave more offspring by mating with more than one female if he is thereby unable to contribute as much to the care and feeding of these offspring. Moreover, it would be of advantage to the female to retain a male for herself since his contribution must increase her reproductive success. Behavioral patterns on the part of the female which have as their function the expulsion of other females from the territory of the male will thus be expected to evolve. Such behavior is well developed in female Redwings. Furthermore, if polygamy has, as a by-product, failure of many mature males to contribute any genes to future generations, there will be strong pressure from these excluded individuals to be admitted to the breeding group. Thus, those males attempting to defend more than one mate will find themselves under increased pressure from other males, a pressure which will be increased the more out of phase his females are, and, hence, the longer period of time they are available for fertilization by another male. Having more than one female will be of no selective advantage to a male if other males successfully inseminate them. Presumably, the stabilized sex ratio observed is the outcome of the interaction between these and perhaps other, as yet unknown, factors.

How they will act to stabilize the system must depend upon the basic ecology of the species and the features of its social system but this has not been investigated in any species.

In species where the male is incapable of contributing much to the welfare of the young, as in many male mammals, the evolution of his role is more easily understood than in such species as blackbirds where this is not the case. In many closely related species, such as meadowlarks and orioles, the males actively feed the nestlings and the Redwing and Tricolor differ markedly in this respect. Since, as will be developed later, the Tricolor is probably an offshoot from the Redwing, the main problem is to determine why the male Redwing lost his role in feeding the young, and why the Tricolor has subsequently regained it. At present there seems to be no satisfactory answer, but certain lines of approach can be suggested.

Polygamy in passerines is characteristic of species occupying habitats in which feeding areas are widespread but nesting sites are restricted. For example, it occurs widely in the ecologically similar savannah-inhabiting ploceids, sturnids and icterids. This is correlated with the evolution of slower maturation rates on the part of the males so that males of some of these species do not breed until they are two years old though females do so when one year old (Friedmann 1949). This type of ecological situation may be very important in shifting the balance in favor of polygamy in species in which the males probably fed the young at the time polygamy was initiated, and may continue to do so. Once polygamy is established, the loss of feeding of the young by the males probably follows in many cases because of the time needed to insure fertilization of all the females, and the importance of extended territory defense when several asynchronous females are present.

The development of sexual dimorphism follows polygamy and promiscuity among icterids (Selander 1959). There must have been an initial advantage enjoyed by the males having a slight development of secondary sexual characteristics so that there was something upon which female selection could have operated (Fisher 1958). As in the development of polygamy, the speed of development of sexual characters is a self-accelerating system which will progress geometrically until it encounters counterselection in the form of an increased mortality rate of the more excessively ornamented males, or their reduced efficiency in caring for their offspring.

The evolution of slow maturation rates in the males poses an even more difficult problem, since such individuals have a much reduced intrinsic rate of natural increase (Cole 1954). In fact, if a male Redwing produces ten offspring per year and no mortality is assumed, the potential production of offspring in four years is reduced from 14,540 for a male beginning to reproduce at the age of one year, to 130 for a male beginning to reproduce at the age of two years. Nonetheless, such a male must leave

more surviving offspring during the period when he is replacing a more rapidly maturing genotype if his genotype is to have selective advantage over one with a faster maturation rate (MacArthur 1960). Slow maturation rates in birds are not correlated with the size of the bird but are characteristic of species in which breeding sites are limited. Probably these are all species which are very ineffectively controlled between breeding seasons so that surpluses of breeding birds are regularly present. Shortage of resources must inevitably be necessary to cause the replacement of rapidly maturing genotypes by more slowly maturing ones, but the exact mechanisms are yet to be worked out.

In the Redwing, the sex ratio of 2-3 ♀♀ per ♂ in the breeding populations studied probably does not reflect the sex ratio in the population as a whole, though the number of males of breeding age is certainly less than the number of females since the males do not breed until they are two years old. The present balance is probably maintained because the advantages to the males of more extreme polygamy are counteracted by the problem of defending successfully a larger territory and preventing stolen copulations as the number of females increases. The females, by defending territories within the territory of the male, exert an active role in determining the number of females able to breed there.

In the Tricolored Blackbird, the situation is quite different because neither sex defends much of an area nor devotes much time to it. The sex ratio here probably mirrors the actual population sex ratio more closely than in the Redwing. With the development of extreme coloniality and the utilization of distant feeding grounds, strong selective pressure in favor of male participation in feeding the young has apparently caused an evolution back toward a more monogamous situation and more equal division of labor between the sexes. However, the tentative nature of these conclusions serves to stress our ignorance about the factors responsible for the evolution of mating systems and maturation rates.

THE EVOLUTION OF BLACKBIRD SOCIAL SYSTEMS

Since no fossil evidence can reveal the nature of social systems in the past, their evolution will probably never be worked out. Nonetheless, certain clues from present-day operation of the systems can be used to suggest conditions likely to have influenced their evolution. Furthermore, in the case of the Redwing and Tricolor, their great morphological similarity leaves little doubt that they are closely related and hence monophyletic. Therefore, the pancontinental Redwing population was probably divided into two isolated groups, one of which evolved into the present day Tricolored Blackbird. In view of the uniformity of the social system of the Redwing throughout its wide range today and the fact that this system is closer to the normal form of organization among passerines, it is probable that the social system at the time of separation was similar to that of the

Redwing today. Therefore, it is the evolution of a nomadic, colonial form of social organization from a more stable, territorial one which calls for explanation.

Today the Tricolored Blackbird is most abundant as a breeding species within the confines of the Great Valley of California where its nomadism is also most pronounced. Breeding is unpredictable, both as to location and size of colonies. To support the food needs of colonies as large as 50,000-200,000 nests, large areas are exploited. Food is gathered chiefly in the shallow water of rice fields, irrigated pastures, ripening and cut grain, and annual grass pastures. The presence of abundant and easily available food is a prime requisite for a successful colony.

At the time of the arrival of European man, conditions in the Great Valley were radically different from today. Dense riparian growth followed all the major watercourses, and on either side of the major rivers were extensive marshes and alkali flats. Prairies and oak parklands covered large areas between the rivers. None of these vegetation types remain today over significant areas and European annual grasses have almost completely replaced the native perennials. Gone, also, are the great numbers of locusts which characterized the grasslands of the valley. Since locusts formed an important item of food for most of the Indians of the Great Valley and surrounding foothills (G. M. Christmas, MS), plagues must have been a regular feature of these areas. It is probable that the locusts also formed the staple food for breeding colonies of Tricolored Blackbirds, as they do today for nomadic, colonial starlings in Asia and Africa (Schenk 1929, 1934, Serebrennikov 1931, Roberts 1940). In the steppes of Asia, locusts are also a staple food for gulls, many species of shorebirds and ducks during the breeding season (Formosov 1937).

Nomadic, colonial social organization in birds evolves most frequently in semi-arid regions of great climatic fluctuations. It is rare in North American birds, but in Australia, for example, 26% of breeding species are nomadic (Keast 1959). For the marsh-nesting Tricolor to evolve such a system, it is necessary that, in addition to unpredictability of breeding areas from year to year, there must be expanses of open feeding grounds surrounding the nesting areas and that these feeding grounds be characterized by an insect population which is very abundant for a short period of time. Without such conditions it is doubtful that the system could operate successfully.

Conditions of instability and broad expanses of open ground surrounding the marshes have probably been characteristic of the Great Valley of California since the early Pleistocene, if not earlier. Instability was produced by the annual winter flooding of large expanses of the valley (Fig. 24). The pattern of flooding and its severity, by changing from year to year, would produce different conditions each breeding season. What were suitable breeding marshes one year might be unsuitable the next and the time

at which areas became suitable would be expected to vary greatly, depending upon the time that winter flood waters receded. Rainfall may have been much greater during the Pleistocene, but since the same trees which now grow in the San Francisco Bay region grew there throughout the glacial period (Chaney 1951), it may be assumed that the climate was still Mediterranean. Thus, the entire present-day

of sufficient ecological differences to permit co-existence. With the Redwing and Tricolor, on the other hand, the contrasting social systems, evolved in response to different environments, result in radically different patterns of environmental exploitation, and thus sympatry might have been achieved in spite of more recent separation.

Certain other evidence favors a more recent separation of the two species. In addition to their morphological similarity and the present day restriction of the Tricolor to California, there is reason to believe that conditions for isolation in California were excellent during the Pleistocene. Several other species pairs are thought to date from this period, e.g., California and Gambel quail (*Lophortyx californica* and *L. gambelii*) and Ladder-backed and Nuttall woodpeckers (*Dendrocopos scalaris* and *D. nuttallii*), and there are many more segregations at the subspecific level. Moreover, there is reason to believe that the grasslands of California have not been as effectively exploited by birds as other grassland areas in North America. There are fewer passerine species which are independent of trees during the breeding season than in any other grassland area (Table 20) so that a marsh-nesting bird might find it more profitable to range further afield in search of food than in areas with more highly developed avifaunas. Thus, though there is no conclusive evidence for choosing between a Pleistocene separation in California or an earlier one, there or elsewhere in western North America, it seems more likely, in the light of evidence now available, that the Tricolor evolved in California, whether early or late.

Today in the Great Valley dams and levees have virtually eliminated extensive winter flooding, most of the vast marshes have been drained, and the alkali flats and prairies are now under cultivation, so that it might be expected that the Tricolored Blackbird, its system no longer adapted to present-day conditions, would be in danger of extinction. Indeed, for a while this was feared to be the case (Neff 1937). However, the attributes of the social system which adapted it to former conditions have actually pre-adapted it to agriculture. For example, the major problem faced by birds utilizing cultivated land is that it is difficult or impossible to nest in many areas which contain rich food supplies. Grain is cut before nesting can be completed, crops are plowed, irrigated pastures are regularly flooded with enough water to drown ground nests, and rice fields are similarly excluded. But Tricolored Blackbirds, being able to concentrate enormous numbers of nests into small areas and to exploit distant feeding areas, are well adapted to utilizing these croplands. Not only this, but their method of communication of food supplies permits them to take advantage of the frequent changes in croplands which make food more readily available. Thus, the Tricolored Blackbird is not only in no danger of immediate extermination, but it is, in fact, one of the passerines best adapted to utilize the abundant supply of insects in agricultural

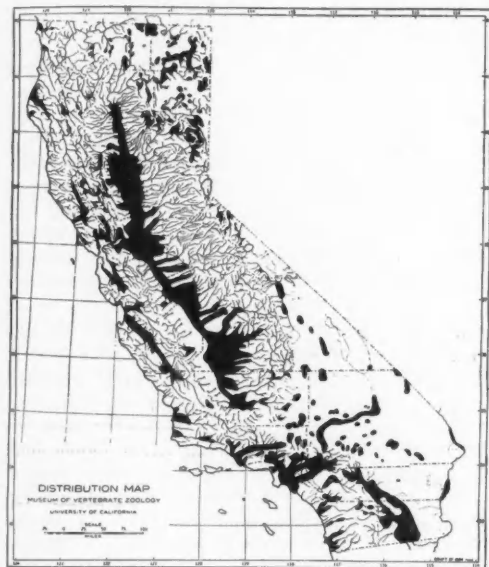


FIG. 24. Areas of California normally subjected to winter flooding.

range of the Tricolor has probably been subject to regular flooding and drying out for long periods of time.

To what extent conditions suitable for Tricolors were present in the Great Basin during the glacial period and earlier is not known. The presence of fossil floras containing species now restricted to California indicates that such conditions might have been more widespread well back into the Tertiary (Axelrod 1958) but the presence of certain plant species does not necessarily imply suitable conditions for year-round exploitation by a complex avian social system. In any case, if the Tricolor formerly had a more widespread distribution than it does today, its range had contracted to California before the arrival of European man in western North America.

A pre-Pleistocene origin for the Tricolored Blackbird is suggested by the distribution of past floras and by the good reproductive isolation of the species. Many species pairs in North America are thought to date from the Pleistocene, but in none of these cases is there extensive sympatry. Often there is considerable hybridization along the narrow zones of contact (Rand 1948). However, it might be argued that, in these cases, conditions during isolation were not different enough to have caused the development

TABLE 20. Breeding passerine birds of North American Grasslands (only those species independent of trees).

Californian Grassland	Southwest Desert Grassland	Great Basin Grassland	Great Plains Grassland
Horned Lark	Horned Lark	Horned Lark	Horned Lark
—	—	—	Sprague's Pipit
Western Meadowlark	Eastern Meadowlark	Bobolink	Bobolink
—	—	Western Meadowlark	Western Meadowlark
—	—	—	Dickeissel
—	—	—	Lark Bunting
Grasshopper Sparrow	Grasshopper Sparrow	Savannah Sparrow	Savannah Sparrow
—	—	Grasshopper Sparrow	Grasshopper Sparrow
—	—	—	Baird's Sparrow
—	—	Vesper Sparrow	Vesper Sparrow
—	Botteri's Sparrow	—	Clay-colored Sparrow
—	Cassin's Sparrow	—	—
—	—	—	McCown's Longspur
—	—	—	Chestnut-collared Longspur

lands of the valleys of California during the breeding season.

SUMMARY

The selective significance of various features of the social organization of the morphologically similar Red-winged and Tricolored blackbirds was studied in north-central California. Data were obtained primarily from simple observation but some field experiments were performed. Particular attention was paid to spatial and temporal aspects of social organization.

Whereas the Redwing breeds throughout most of temperate North America, the Tricolor is virtually restricted to the lowlands of California, but it is nomadic within its narrow range. Outside the breeding season both species are highly gregarious.

Male Redwings begin to establish territories in north-central California in early January, but until late March or early April the territories are occupied only in the early morning and late evening. Nest-building begins in early or mid-April at most sites; but females become out of phase with each other and nesting in any given marsh extends over long periods of time. Nesting habitats include emergent vegetation (particularly cattails), ditch banks, roadsides, fencerows, riparian vegetation, weed and brush patches, cropland, and occasionally upland stands of chaparral and grass. In cropland, however, most nests are destroyed by harvesting before fledging can be completed and reproductive success is poorer than in the marshes.

There is a general correlation between the size of Redwing territories and the proportion of food obtained within their confines, but food is probably not the proximate factor by which territory size is regulated. That territorial behavior strongly limits breeding density is suggested by (a) the frequency and severity of territorial challenges, (b) the regular occupation by newcomers of the territories of birds held for a few hours in a trap, and (c) the rapid and regular reoccupation throughout the breeding season of territories from which the occupants have been removed. Normally, first-year males do

not maintain territories and breed but some may occupy areas from which the adults have been shot. Sex ratios among breeding birds are difficult to determine but on certain study areas there were 2.8-3.7 ♀♀ per ♂, with a range of 1 to 6. Usually the role of the male is confined to territorial defense and insemination of the females, but a few males occasionally or regularly feed the nestlings.

In contrast, territories are not established by male Tricolored blackbirds until the morning of the day breeding begins, and territories are only about 35 sq ft in area. Moreover, nesting is usually highly synchronous, all nests being constructed within the period of one week even in colonies as large as 50,000-100,000 nests. Some colonies, however, grow peripherally. As in the Redwing, most nests are placed in emergent vegetation but the birds also use grain, alfalfa, and safflower fields, mustard patches, ditchside vegetation, and occasionally trees. Breeding begins in April and May, being earliest in the foothills and latest in the rice growing country, in both cases being timed to optimal feeding conditions. To feed the enormous numbers of young involved, adults fly as far as four miles and more than 30 sq mi of land may be exploited by a single colony. The males actively feed the young but in other respects the mating system resembles that of the Redwing.

Sometimes colonies are completely destroyed by predators and at other times mass desertions, which may be related to poor food supplies, occur. Territorial behavior cannot limit the sizes of breeding colonies but several lines of evidence suggest that colony size is nonetheless adjusted to the capacities of the environment. Apparently an assessment of the environment is made during the period of colony establishment by means of mass feeding flights but the exact mechanism remains obscure. Thus, whereas in neither species is there a 'food territory' in the classical sense, the spacing within the systems as a whole is intimately related to environmental exploitation.

Combining assumptions regarding the energy demands of various activities and the tabulation of field data on activity sequences, tentative time and energy

budgets for the two breeding systems are constructed. The colonial system of the Tricolor is more demanding of energy, because of the great energy expended in flight to distant feeding grounds but less demanding of time. Moreover, the colonial system is more exacting of high concentrations of food supplies which may help to explain the peculiarly spotty distribution of breeding colonies. The value of early occupation of territories by male Redwings is discussed.

Theoretical arguments and field data support the idea that the primary sex ratio in the polygamous Redwing is equality and it is shown that selection can easily favor polygamy despite equal sex ratios. Thus the evolution of polygamy cannot be viewed as the product of unbalanced sex ratios but must be considered on its own merits. Ecological factors favoring monogamy and polygamy are discussed and evaluated and it is concluded that the evolution of slow maturation rates in male blackbirds and other species must inevitably be related to the presence of surplus breeding populations.

The colonial system of the Tricolor probably evolved in California in response to the instability produced by regular winter flooding of its breeding range and the concentration of food provided by locust plagues. The time of separation from the pancontinental Redwing population is uncertain but it may be as recent as the Pleistocene. The features of the colonial social system of the Tricolored Blackbird which adapted it to former conditions have preadapted it for utilizing agricultural lands as well.

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